PALÆONTOGRAPHICAL SOCIETY.

VOL. LXXIV.

THE PALÆOZOIC ASTEROZOA.

PART V.

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THE CARBONIFEROUS INSECTS.

PART II.

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Title-page and Index.

THE PLEISTOCENE MAMMALIA —HIPPOPOTAMUS.

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ISSUED FOR 1920.

PALÆONTOGRAPHICAL SOCIETY.

VOLUME LXXIV.

CONTAINING

ISSUED FOR 1920.

LONDON:
PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.

AGENTS FOR THE SOCIETY

DULAU AND CO., LTD., 34-36, MARGARET STREET, CAVENDISH SQUARE W 1.

JULY, 1922.

THE PALÆONTOGRAPHICAL SOCIETY was established in the year 1847, for the purpose of figuring and describing British Fossils.

Each person subscribing ONE GUINEA *is considered a Member of the Society, and is entitled to the Volume issued for the Year to which the Subscription relates. The price of the Volume to Non-subscribers is* TWENTY-FIVE SHILLINGS NET.

Subscriptions are considered to be due on the 1st of January in each year.

The Annual Volumes are now issued in *two forms of Binding:* 1st, with all the Monographs stitched together and enclosed in one cover; 2nd, with each of the Monographs in a paper cover, and the whole of the separate parts enclosed in an envelope. Members wishing to obtain the Volume arranged in the LATTER FORM are requested to communicate with the Secretary.

Most of the *back volumes* are in stock. Monographs or parts of Monographs already published can be obtained, apart from the annual volumes, from Messrs. DULAU AND CO., LTD., 34–36, Margaret Street, London, W. 1, who will forward a complete price list on application.

Members desirous of forwarding the objects of the Society can be provided with plates and circulars for distribution on application to the Secretary, Dr. A. SMITH WOODWARD, British Museum (Nat. Hist.), South Kensington, London, S.W. 7.

The following Monographs are in course of preparation and publication:

The Cambrian Trilobites, by Mr. Philip Lake.

The Carboniferous Insects, by Mr. Herbert Bolton.

The Palæozoic Asterozoa, by Dr. W. K. Spencer.

The Pliocene Mollusca, by Mr. F. W. Harmer.

The Pleistocene Mammalia, by Prof. S. H. Reynolds.

Owing to scarcity of paper, the Council has decided to omit from the present volume the usual lists of members and publications. Full particulars can be obtained from the Secretary.

Members deceased during 1920: Lieut.-Col. Linley Blathwayt, Dr. J. Alfred Codd, Ernest Gibson, Esq., M. R. Pryor, Esq.

New members: E. B. Bailey, Esq., Dr. F. Corner, F. G. Collins, Esq., Dr. G. W. Lee, Murray Macgregor, Esq., Arthur Wrigley, Esq., and Peking Union Medical College.

ANNUAL REPORT OF THE COUNCIL

FOR THE YEAR ENDING 31st DECEMBER, 1919.

READ AND ADOPTED AT THE

ANNUAL GENERAL MEETING,

HELD AT THE APARTMENTS OF THE GEOLOGICAL SOCIETY, BURLINGTON HOUSE,

4th JUNE, 1920,

E. T. NEWTON, Esq., F.R.S., Vice-President,

IN THE CHAIR.

The Council, in presenting its Seventy-Third Annual Report, regrets that, owing to present difficulties, its publications are still in arrear; but volume No. LXXII for the year 1918, containing an instalment of the Monograph of Pliocene Mollusca, and the first part of a Monograph of British Bellerophontacea, is now nearly ready, while most of the material for Volumes LXXIII and LXXIV has already been received, and many of the illustrations have been prepared. It is proposed to issue the two latter volumes, which are for the years 1919 and 1920, as nearly as possible together, the first containing an instalment of the Monograph of Pliocene Mollusca, the concluding part of British Bellerophontacea, and the first part of a Monograph of Carboniferous Insects, the second containing instalments of the Monographs of Pleistocene Mammalia (Hippopotamus), and Palæozoic Asterozoa, with the concluding part of the Monograph of Carboniferous Insects.

The expenditure during the year has been much less than the income, but this is due mainly to the delay in publication already mentioned, partly to the inclusion of Messrs. Dulau's delayed cheque for £30 11*s.* 1*d.*, received in 1919 for the year 1918. When the Society's volumes are brought up to date, it will be necessary to use at least the greater part of the sum of £610 10*s.* 6*d.*, which is still temporarily invested in War Loan and Exchequer Bonds. The thanks of the Society are due to Mr. F. W. Harmer for a gift of 15 guineas towards the cost of the plates illustrating his Pliocene Mollusca.

Among members who have died during the year, the Council desires especially to refer to Prof. Charles Lapworth, Mr. John Hopkinson, Mr. Ernest Gibson, Col. Linley Blathwayt, Mr. M. R. Pryor, and Dr. J. Alfred Codd. Prof. Lapworth will always be held in grateful remembrance by the Society for the great Monograph of British Graptolites which he planned and edited; and Mr. John Hopkinson will be remembered for his long and valuable services on the Council, by whom he was most highly esteemed. A few new members have joined the Society, but many more are needed to replace the losses during recent years.

The thanks of the Society are due to the Council of the Geological Society for permission both to store the stock of back volumes, and to hold the Council Meetings and Annual General Meeting in their apartments.

In conclusion, it is proposed that, in addition to the late Mr. John Hopkinson, the retiring members of the Council be Mr. G. Barrow, Mr. W. P. D. Stebbing, and Prof. W. W. Watts; that the new members be Mr. R. G. Carruthers, Prof. E. J. Garwood, Dr. W. D. Lang, and Dr. W. K. Spencer; that the President be Dr. Henry Woodward; the Treasurer, Mr. Robert S. Herries; and the Secretary, Dr. A. Smith Woodward.

Annexed is the Balance-sheet.

The PALÆONTOGRAPHICAL SOCIETY in account with ROBERT S. HERRIES, Esq., M.A., F.G.S., Treasurer.

Cr. *From January 1st, 1919, to December 31st, 1919.* *Dr.*

		£	s.	d.	£	s.	d.
Balance from last Account					34	3	5
Members' Subscriptions—1914–1918	160	168	0	0			
" " 1919	109	114	9	0			
" " 1920–1921	7	7	7	0			
	276				289	16	0
Carriage paid by Members					0	11	8
Sales of back stock to Members					68	7	7
Sales by Messrs. Dulau & Co., Ltd.					88	1	5
Repaid Income Tax (1 year)					11	14	0
Gift from F. W. Harmer, Esq.					15	15	0
Dividend on £500 Natal 3 per cent. Stock (less income tax)					10	10	0
Divideud on £210 10*s.* 6*d.* 5 per cent. War Loan					10	10	6
Dividend on £400 6 per cent. Exchequer Bonds (less income tax)					16	16	0
					£546	5	7

	£	s.	d.	£	s.	d.
Printing, binding, distribution, etc., Vol. LXXI				181	6	7
Drawing illustrations and preparing blocks				121	12	6
Collotype and lithographic printing				43	19	0
Secretary's honorarium				52	10	0
Postage and stationery				4	10	3
Premiums, Fire Insurance				1	5	6
Petty charges—Porter	1	0	0			
Bank	0	3	4			
				1	3	4
Balance at Bank				139	18	5
				£546	5	7

We have examined the above account, compared it with the vouchers, and find it to be correct; we have also seen the receipt for £500 Natal 3 per Cent. Consolidated Stock, and for the £210 10*s.* 6*d.* 5 per cent. War Loan, and £400 6 per cent. Exchequer Bonds, the last converted into $5\frac{3}{4}$ per cent. Exchequer Bonds, February, 1920.

Henry A. Allen
R. G. Carruthers
E. T. Newton.
R. L. Sherlock.
} Auditors.

Robert S. Herries,
Treasurer.

April 26th, 1920.

Council and Officers elected June, 1920.

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Secretary.

A. Smith Woodward, Esq., LL.D., F.R.S., British Museum (Nat. Hist.), South Kensington, London, S.W. 7.

Palæontographical Society, 1920.

A MONOGRAPH

OF THE

BRITISH PALÆOZOIC

ASTEROZOA

BY

W. K. SPENCER, M.A., D.Sc., F.G.S.

PART V.

Pages 197—236; Plates XIV—XVII.

LONDON:

PRINTED FOR THE PALÆONTOGRAPHICAL SOCIETY.

July, 1922.

PRINTED BY ADLARD AND SON AND WEST NEWMAN, LTD., LONDON AND DORKING.

Since I wrote the previous pages my attention has been called to the important work of Petersen and his colleagues (104), which, by its exact information on the feeding habits of recent forms, enables us to judge with more certainty as to the mode of life of their fossil relatives. In particular it helps us to understand the differentiation which has arisen among the forms we are now considering. It always seemed surprising to me that, in the older Palæozoic rocks, the true Asteroid forms (carnivorous) were relatively few in number, and not so much differentiated as the forms which were either Ophiuroidea or transitional towards the Ophiuroidea as judged by the manner of growth of the interradial areas—a feature associated (see above, p. 195) with the mud-eating habit. Petersen's observations show that, even to-day, the mud-eating habit is the general rule among the lower animals which live on the sea-bottom, and that it is plant detritus in the uppermost layer of mud which provides the nourishment. The plant detritus in Danish waters is formed from grass-wrack (*Zostera*) and its attendant microflora living under the water. This plant produces "in leaves alone 8,232,000 kg. annually in the Danish waters east of the Skaw. In course of time these plants of the benthos formation die, or are torn away by the currents or action of the waves, and carried out, in whole pieces or fine particles, into the deeper water, where they are deposited on the bottom in the form of detritus" (1914, p. 46). Here they form an uppermost brown layer of the mud, "especially well suited as nourishment for the animal life of the sea-bottom." The animals which feed on the plant detritus in the brown mud may live either buried in the bottom or not buried in the bottom.

This is well illustrated by the following picture of the mode of life of the Echinodermata given 1914, pp. 61—64:

(1) Those without arms, and living buried in the bottom.

ECHINOIDEA IRREGULARIA without masticatory organs (ATELOSTOMATA):

Brissopsis lyrifera, Forb. *Echinocardium flavescens*, Müll.
Echinocardium cordatum, Pennant. *Spatangus purpureus*, Müll.

"All these are typical detritus-eaters, feeding directly on the upper layer of the bottom, without any previous sorting of the detritus. As the aquarium observations have shown, they live buried in the bottom, maintaining communication with the surface by means of vertical tubes, and drawing down their food by means of the far-reaching ambulacral feet . . . the *Echinocardium cordatum* frequently devours, together with the bottom detritus, numbers of quite small young bivalves . . ."

(2) Very mobile arms; living buried in the bottom.

Amphiura chiajei, Forb. *Amphiura filiformis*, Müll.

"The *Amphiura* species live, as I have frequently observed in aquaria, buried deep down in the bottom, only the extremities of some of the arms reaching up over it. These extremities are in constant movement, feeling about over all the small particles in the vicinity, and now and again coiling round and grasping some few of them, the food being then drawn down beneath the surface of the bottom to the mouth. . . . I have examined several hundreds of specimens taken at different places and seasons, without ever finding anything in their stomachs beyond more or less finely sorted bottom detritus, with the micro-organisms and skeletal parts therein contained. . . . Possibly they may, like *Echinocardium cordatum*, accidentally encounter small young molluscs and pass the same into their stomachs together with the detritus of the bottom. . . ."

(3) More or less mobile arms; not living buried in the bottom.

a. Ophiuroidea.

Arms only slightly mobile: *Ophiothrix fragilis*, Abgd., *Ophiopholis aculeata*, Müll.

Arms very mobile: *Ophioglypha* (five species).

"The two first-named species, which in aquaria often sit motionless for days in their hiding-places, are, in conformity with this, mainly detritus-eaters; they can, however, according to Eichelbaum, also devour animal food. This writer has found in the contents of the stomach indubitable remains of worms (soft parts with setæ still attached), crustaceans, remains of small Echinoderms and young bivalves, besides detritus.

"The *Ophioglypha* species, on the other hand, which have very mobile arms, and will in aquaria fling themselves with astonishing rapidity and accuracy upon pieces of meat, small molluscs and similar animal food, are distinctly carnivorous detritus-eaters. They are often found with remains of small molluscs or crustaceans in the stomach; on examining a quantity of specimens, however, a comparatively large number will always be found quite empty. Experience has shown this to be a good sign that the animal in question is carnivorous; the greater the extent to which an animal is constrained to live on prey, the greater will be the percentage found with perfectly empty stomachs, evidently on account of the length of time which frequently elapses between one capture and the next. The *Ophioglypha* species, besides animal food, also eat detritus.

"*O. texturata* lives, for instance, in the Limfjord, where it is found at most places in quantities (up to 71 specimens per 0·1 m^2.) almost entirely on detritus, as a rule with a number of large bottom diatoms. In the Kattegat, on the other hand, the species feeds chiefly on small bivalves such as *Abra alba*, small Crustaceans such as Gammaridæ, Mysidæ and *Diastylis*, the young of *Echinocardium* and winged insects (probably bees)! The last find indicates that they occasionally condescend to feed on carrion. . . . Finally *Ophioglypha* occasionally devours smaller specimens of its own species."

b. ASTEROIDEA. Arms slightly mobile.

Asterias rubens, L.	*Astropecten mülleri*, Müll. et Tr.
Solaster papposus, L.	*Cribrella sanguinolenta*, Müll.
Solaster endeca, L.	

"All these animals are distinctly carnivorous." (It is shown that they will live on Mollusca, Gasteropoda, Crustacea, Worms, Bryozoa, *Echinus* and other Echinoderma. No animal is safe from the attacks of *Asterias*, which also devours carrion in large quantity.)

Petersen also shows (1918, p. 14) that "where the sea bottom is level, *i.e.* formed of fine sand, clay or mud without foreign bodies of any considerable size, the animal population is uniform throughout large tracts," which can be compared with the different vegetation tracts on land such as meadowland, moorland, cultivated fields and the like. These uniform populations he calls *animal communities*, and suggests that it is a combination of local physical conditions with the interplay of the various organisms which determines the constitution of these communities. Thus *Echinocardium* is replaced by *Brissopsis* as a sandy bottom passes into clay, and "it is remarkable to note how in those communities where *Amphiura* spread their arms abroad, forming a network in the bottom, extremely few bivalves are found at all. The young will here doubtless as a rule be devoured while still quite small by the *Amphiura*, and only a few individuals of certain species manage to survive" (1918, p. 17).

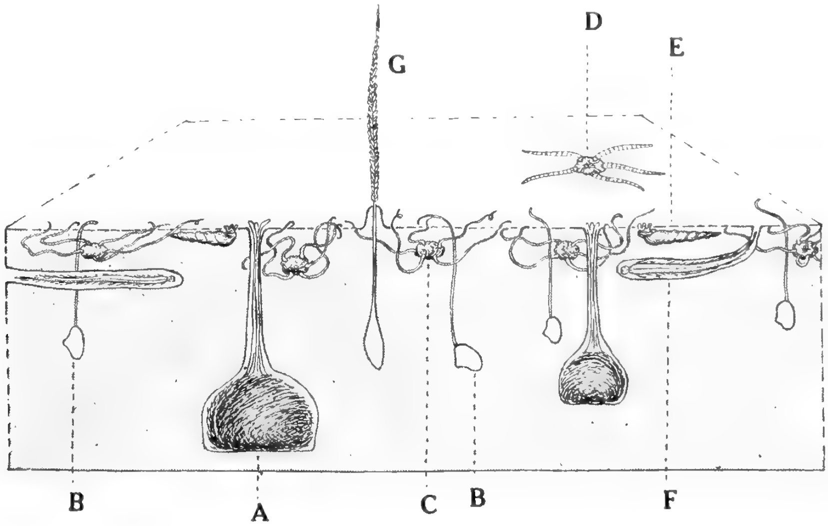
It seems to me that Petersen might have carried his comparison with the land-flora a stage further, and compared a section across the bottom to that of a section through the soil of a copse, where each layer of soil is being made use of by the plants, the deepest layers being occupied by the roots of trees, the next layers by bulbs, and the surface layers by shallow-seated rhizomes or the roots of grass. I have given here (Text-fig. 139) an imaginary cross-section through an *Echinocardium-Turritella* community, based on Petersen's observations, to show such a comparison. The distinction between the animal and the vegetable communities lies in this, that whereas the plants obtain their salts from their own layer of soil, the animals, with one exception, all obtain their nourishment from the uppermost layer of the mud. Nevertheless it is clear that the occupation of the various levels of the bottom gives greater opportunity for the living together of a mass of organisms, provided that the supply of food be sufficient. We may compare the community with a town population living in flats, all being supplied with food brought from the surrounding country area.

Certain forms seize the detritus as it is falling to the bottom. *Modiola*, *Mytilus edulis* (the edible mussel), so familiar on the supports of piers, have this power. A fauna which consists mostly of organisms of this nature is named by Petersen an *Epifauna*, and it is present (*a*) when the current is sufficiently strong to wash the stones at the bottom free of mud and so allow attachment of the mussels, etc., or (*b*) where there are rocks or harbour works sticking up in the water. An Epifauna is often rich in Echinodermata. Some Asterozoa, *e. g. Gorgonocephalus*, and, I believe, *Brisinga*, are important characteristic forms.

We can use this material to reconstruct the mode of life of the fossil Asterozoa. Consider first the forms which *lie buried in the mud.*

(1) These probably will be well preserved, since their bodies will not after death be subject to dissolution by the action of currents or by the carrion-eating animals of the surface of the bottom.

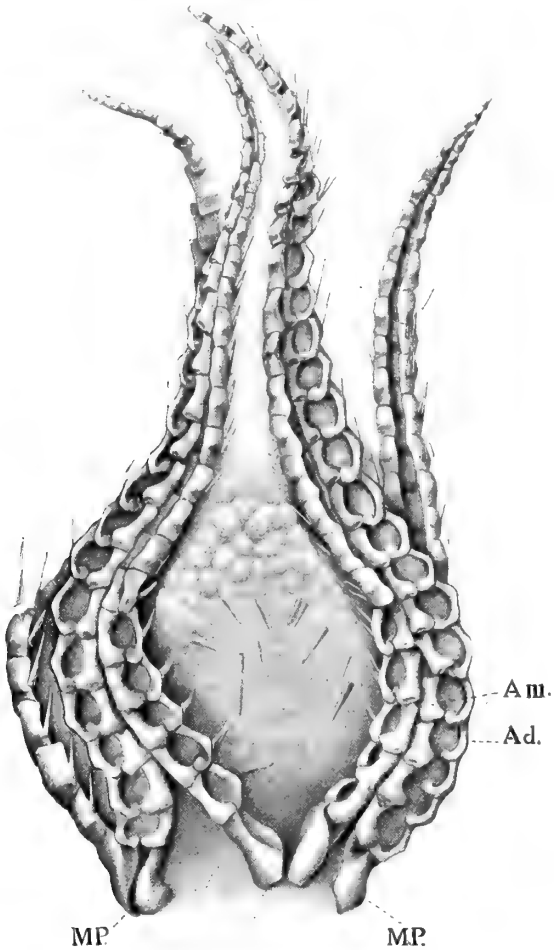
(2) They may be expected to die occasionally in some characteristic attitude. The surrounding mud would support the arms and so retain the attitude.



TEXT-FIG. 139.—Drawing of a cross-section through an *Echinocardium-Turritella* community (kindly drawn for me by Magister Blegvad as a modification of a sketch I submitted to him). *A., Echinocardium cordatum* (a burrowing sea urchin); *B., Abra nitida* (a Lamellibranch); *C., Amphiura filiformis* (a burrowing Ophiurid); *D., Ophioglypha texturata* (a surface Ophiurid); *E., Turritella terebra* (a burrowing Gasteropod); *F.*, a worm; *G., Virgularia mirabilis* (an Anthozoan).

The forms of the genus *Protaster* and its allies offer most striking examples of this. They are frequently found, as both Ruedemann (1912, p. 90) and Stürtz (1890, p. 234) have observed, with their arms flexed vertically to the disc (Text-fig. 140). It is clear that it is the same attitude as that described by Petersen (1913, p. 26) for *Amphiura*, which "lies with the body and most of the arms deep down in the clay, but always with the tips of one or more arms stretched out ready to finger any object that comes near and if wanted to draw it down into the clay, where it is swallowed." Petersen also points out that the *Amphiuræ* lie in such quantities that they form a dense net over the sea bottom. The occurrence of *Protaster* or its relations in abundance on the same slab, has been noted by several authors, and we now see the explanation that it was when alive a "detritus"-feeder with the same habits as *Amphiura*. I have noted these facts in advance of my description of *Protaster*, for I feel that it gives one confidence that we can learn much from the manner in which forms are preserved.

Among the forms with which we are immediately concerned, we may bring to notice *Palasterina* and *Schuchertia*. *Palasterina* is found in crowded masses (Pl. XVII, fig. 3) in a very complete condition, and there can be no doubt that it dug itself into the mud. In support of this we may note that the Devonian form,



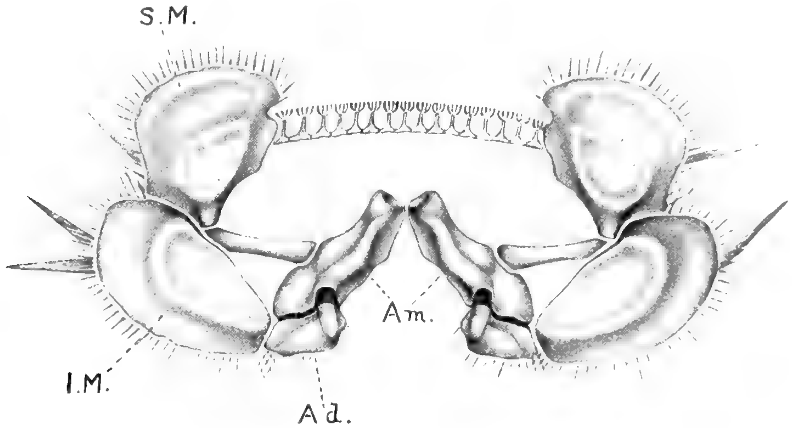
TEXT-FIG. 140.—Drawing of one of the cotypes of *Protaster* (*Tæniaster*) *spinosus*, Billings (Ottawa Mus. no. 1404 *b*). *Ad.*, adambulacral ; *Am.*, ambulacral ; *M.P.*, mouth-angle plate. × 10.

P. follmanni, is found with its arms lightly flexed over its disc (Pl. XVI, figs. 6, 7). *Schuchertia* on the contrary (see p. 210) probably lived buried just beneath the surface.

(c) *Marginal Plates and their Relationship to the Shape of the Arms.*

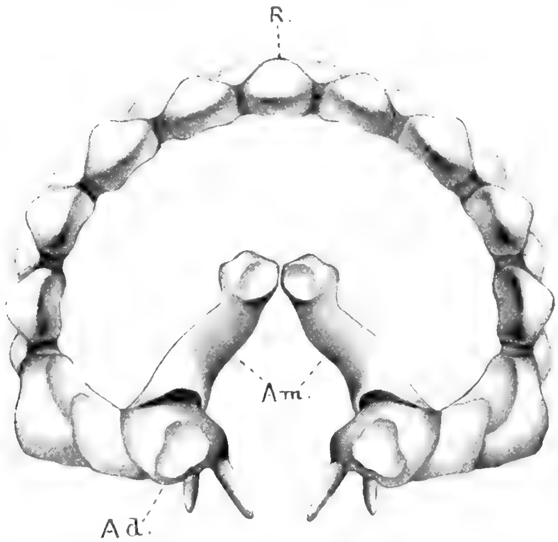
It is useful at this point to examine the exact importance of the presence or absence of differentiated marginalia. It seems to me that such plates in fossil forms are a help in determining the original shape of the arms, but of little value in classification.

If we examine modern genera we find that strongly differentiated marginalia are only found in forms like *Astropecten*, which have an arm almost rectangular in cross-section (Text-fig. 141). When a genus possesses a rounded arm, *e. g. Nardoa*



TEXT FIG. 141.—Cross-section through the arm of a recent *Astropecten*. *Ad.*, adambulacral; *Am.*, ambulacral; *I.M.*, infero-marginal; *S.M.*, supero-marginal.

(Text-fig. 142), the differentiation tends to become obscured. This may be explained as follows: In the rounded arm there is no physical reason why any one ossicle should be larger than another, provided that they all commence to be laid down at



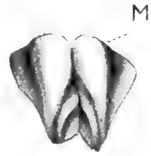
TEXT-FIG. 142.—Cross-section through an arm of a recent *Nardoa*. *Ad.*, adambulacral; *Am.*, ambulacral; *R.*, radial.

the same moment, for each ossicle has ample room to grow and the rows are not subject to unequal lateral pressures. In an arm with angles at the side, especially when the ossicles are crowded and consequently exercising pressure on one another, the masses of calcite will tend to be pushed into the angles, where larger plates will be built up.

A good example of the artificiality of the use of the marginal plates as a feature of primary importance in classification is seen in the case of the recent family Linkiidæ, which is placed by Sladen among the Cryptozonia, in spite of the fact that the forms within the family belong to one of the great primary groups of the Asteroidea, namely the Valvata, the majority of which are typically Phanerozonate. Almost all the genera within the family have rounded arms, but when, as in *Fromia*, the arms are angular, differentiated marginalia are present.

Text-fig. 143.—Adoral view of a mouth-angle of *Schuchertia wenlocki* (from Royal Scottish Mus. no. 485). *Ad*, first adambulacral; *M.P.*, mouth-angle plate; *O.*, odontophor. × 10.

It is possible that young forms may show differentiated marginalia and that this differentiation may be lost in the older more mature specimens. In consequence of this, Ludwig and others have stated as a general law that all Cryptozonate forms have descended from Phanerozonate stock. Rather would the explanation appear to be, that the so-called differentiated marginalia are the first-formed plates, which obtain a start over the others and for some time remain distinguishable. As the forms become more mature, the other rows of plates,



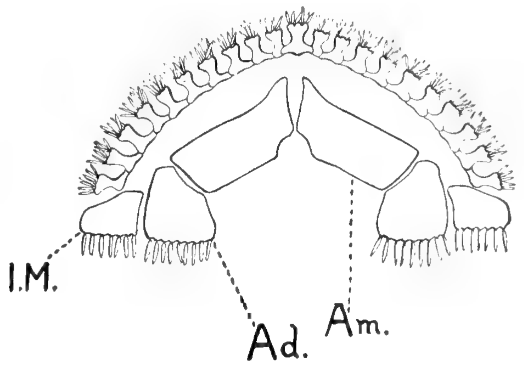
Text-fig. 144.—Adoral view of a pair of mouth-angle plates (*M.P.*) of *Palasterina primæva* (from specimen in Mus. Pract. Geol.). × 10.

provided that they have room to grow, catch up the early-formed plates, and the distinction is lost.

If the general argument be correct, we can use the changes in the shapes of the marginal (or equivalent) plates to show that the general tendency of evolution in the *Schuchertia*-lineage is to develop a flattish body, while in the *Palasterina*-lineage the arms become progressively rounder.

(d) *The Genera within the Family Eoactinidæ.*

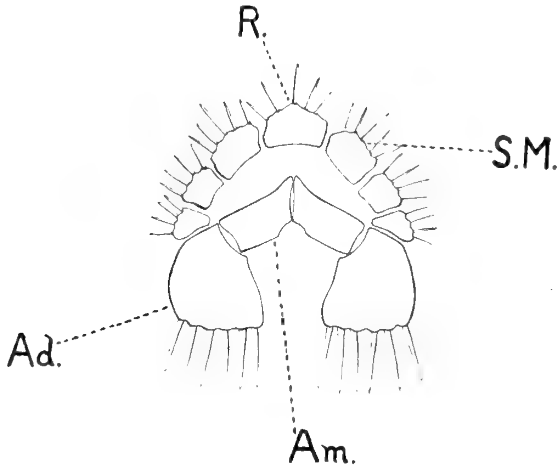
The general features of the Eoactinidæ have been mentioned already (p. 178). Their most obvious characters are the marked Asteroid shape, the broad adambulacralia, and the simple flooring-plate character of the ambulacralia. Although the forms are transitional between the early Asterozoa and the true Ophiuroidea, it must not be assumed that any of their descendants became typical Ophiuroidea. Those Eoactinid genera which we know adequately are specialised forms, which go through their own lineage-development and die, without leaving, so far as we can judge, any descendants.



TEXT-FIG. 145.—Diagrammatic cross-section through the arm of *Schuchertia wenlocki*. *Ad.*, adambulacral; *Am.*, ambulacral; *I.M.*, infero-marginal. × 10.

Much material is known of Eoactinidæ. Nearly the whole of this divides into two lineages, each of which can be confined to one genus. These two genera are:

Schuchertia, Gregory, found both in Britain and America, and ranging from the Middle Ordovician to the Middle Silurian.



TEXT-FIG. 146.—Cross-section through the arm of *Palasterina primæva*. *Ad.*, adambulacral; *Am.*, ambulacral; *R.*, radial: *S.M.*, supero-marginal. × 10.

Palasterina, McCoy, found in Britain, Sweden and Germany, and ranging from the Middle Silurian to the Lower Devonian.

A distinctive feature between the two lineages is the shape of the mouth-angle plates, figured in Text-figs. 143 and 144.

In addition, as mentioned above, *Schuchertia* has a flattish arm and well-differentiated infero-marginalia, while in *Palasterina* the arms are much more rounded.

In addition to these two lineages there is a form, known from one specimen only, which I have named *Eoactis*. It is not a *Schuchertia*, and differs from *Palasterina* in certain features which may prove to be only "age" features. At present, however, I am disposed to give these features a somewhat greater value.

A fourth genus is a multi-armed form known only from the Bundenbach slates. It has been placed by Stürtz in several genera and species. I am following Schuchert in only recognising one genus and species, *Palæosolaster gregoryi*, Stürtz. On the whole the affinities of this form are with *Palasterina* rather than *Schuchertia*, but we cannot say at present that it is merely a multi-armed *Palasterina*.

The genera of Eoactinidæ may be defined as follows:

Eoactis, Spencer. Mouth-angle plates rounded; arms straight; a very few flat infero-marginalia in interradial angles.

Schuchertia, Gregory. Mouth-angle plates narrow, high; arms straight and flat; both infero-marginalia and adambulacralia recognisable on oral surface.

Palasterina, McCoy. Mouth-angle plates swollen; arms petaloid and rounded; adambulacralia bounding oral surface.

Palæosolaster, Stürtz. Multi-armed; mouth-angle plates narrow and high; adambulacralia bounding oral surface; arms rounded; lateral and oral surface of arm covered with small well-separated plates, each of which carries a long spine.

Genus **EOACTIS**, Spencer.

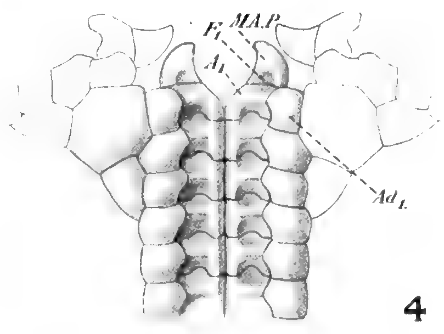
1914. *Eoactis*, Spencer, Brit. Palæoz. Asterozoa (Mon. Pal. Soc., vol. for 1913), p. 30.
1915. „ Spencer = ? *Urasterella*, Schuchert, Bull. 88, U.S. Nat. Mus., pp. 173, 178, 186.
1915. „ Bather, Geol. Mag. [6], vol. ii, p. 320.
1916. „ Hudson, New York State Mus. Bull. 187, Twelfth Report of the Director, 1915, p. 135.

Generic Characters.—See above.

I commence my account of the members of this family by a description of the form which I have named *Eoactis simplex* (see p. 30). It is known only from one specimen and is from a comparatively high geological horizon. It may be the young form of a species not yet recognised. Nevertheless it serves as a convenient starting-point in the discussion of the origin and relationships of the other species.

The form is almost diagrammatically simple. The groove is floored with ambulacralia of the flooring-plate type. Alongside these are stout adambulacralia. The mouth-angle plates have no distinctive shape like those of *Schuchertia* or *Palasterina*. There are a few other skeletal plates visible on the oral surface. In the axils of the arms is a stout polygonal odontophor, and on each side of it a definitely recognisable flat infero-marginal. The apical surface is unknown, but a lateral view of one of the arms towards the extremity shows that there was a covering of small plates.

The structure of the oral interradial area, inasmuch as only the odontophor and proximal infero-marginalia are present, suggests in a generalised way the structure of a *Urasterella* (compare Text-fig. 86, p. 134). In fact, Schuchert (1915, p. 186), from the very slender account of the species given by me in the Introductory Section to this Monograph, imagined that it might belong to a



TEXT-FIG. 147.—Drawing (somewhat diagrammatic) of *Eoactis simplex* (reproduced from Plate I, fig. 4). A_1, first ambulacral; Ad_1, first adambulacral; F_1, cup for first tube-foot; *M.A.P.*, mouth-angle plate.

Urasterella. I do not know any *Urasterella* which shows such a very definitely differentiated first pair of infero-marginalia, and there is no evidence of the "*Urasterella* paxilla." I regard its generalised features as being those common to very many primitive Asterozoa, and consider that we can most pertinently regard it as illustrating the structure of the basic member of a series which gave rise to *Schuchertia*, *Palasterina* and *Palæosolaster*, each of which tends to depart more and more from the "primitive Asterozoan" appearance as a specialised mode of life is acquired.

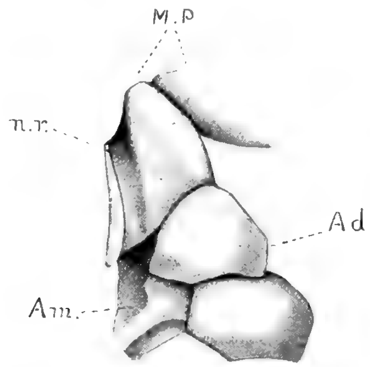
1. **Eoactis simplex,** Spencer. Plate I, fig. 4; Plate XV, fig. 8; Text-figs. 147, 148.

1914. *Eoactis simplex*, Spencer, Brit. Palæoz. Asterozoa (Mon. Pal. Soc., vol. for 1913), p. 30, pl. i, fig. 4.
1915. *? Urasterella girvanensis*, Schuchert, Bull. 88, U.S. Nat. Mus., pp. 173, 178, 186.
1915. *Eoactis simplex*, Bather, Geol. Mag. [6], vol. ii, p. 320.

Material.—One impression in the British Museum (Nat. Hist.), no. E. 13154, originally no. 657 of the G. H. Morton Collection. The oral surface only is shown.

Specific Characters.—As those for genus.

Description.—Text-fig. 147, which is reproduced from Pl. I, fig. 4, of this Monograph, illustrates most of these characters. The groove is open and shows ambulacralia which are similar to those of *Schuchertia* (Text-fig. 124, p. 183), except that the overlap of an ossicle on its predecessor is more pronounced. The adambulacralia are broad, with an evenly swollen surface. One can just trace a pustular ornament. The proximal adambulacralia are not differentiated either in size or shape. They fit together so that the suture gives the appearance of a twisted rope, exactly as is described as a generic character for the American form *Schoenaster fimbriatus*, Meek and Worthen. I find that this character also occurs in some species of *Aspidosoma*. The odontophor is large and prominent with a swollen unornamented surface. It terminates proximally in a point which does not quite reach the mouth-angle plates. A small ossicle intervenes here exactly as is figured by Hudson (33, for *Hudsonaster narrawayi*, reproduced in this Monograph, Pl. I, fig. 5). This small plate is not shown in the text-figure.



TEXT-FIG. 148.—Drawing of the mouth-region of *Eoactis simplex*. *Ad.*, adambulacral; *Am.*, ambulacral; *M.P.*, mouth-angle plate; *n r.*, groove for nerve-ring. × 20.

An infero-marginal fits on each side of the odontophor. Beyond this the infero-marginal series disappears on to the apical surface. The extremity of the arm pointing west in the photograph (Pl. XV, fig. 8) shows one or two stout plates in apical view which probably belong to this series.

Dr. Bather (*loc. cit.*) makes the following remarks about my original description of the mouth-frame: "As an example of a very primitive mouth-frame, Mr. Spencer (1914, p. 30) takes the fossil which he names *Eoactis simplex*. His drawing (Pl. I, fig. 4) shows a simple series of ambulacrals and adambulacrals. At the proximal end of the groove the ambulacrals diverge, and the series is there terminated on each side by a curved subtriangular plate, which Mr. Spencer designates 'mouth-angle plate.' It is, however, clear from his drawing, no less than from the specimen itself, that this plate continues the ambulacral series and not the adambulacral, and this is further emphasised by the fact that the depression for the first podium lies equally on this plate and on the adjacent ambulacral. Further examination of other interradii in the fossil showed that this ambulacral mouth-angle plate was actually overlaid by a paired adambulacral element, though only the empty space that might have been occupied by such a plate is shown in the drawing. It follows from this that the plates marked by Mr. Spencer as A_1 and Ad_1 were really A_2 and Ad_2, and that the true proximal ambulacral and its corresponding adambulacral had not yet fused to form a mouth-angle plate."

I have introduced a new drawing (Text-fig. 148) which shows the mouth-angle plate in one of the interradii mentioned by Dr. Bather as showing the plate in two pieces. It will be seen that the plate is in one piece and has precisely the same structure as the mouth-angle plate of the recent *Astropecten* figured in Text-fig. 137, p. 195. The suture which Dr. Bather thought that he could distinguish separating two elements is obviously the groove for the nerve-ring. Dr. Bather allows me to say that he accepts this explanation.

Measurements.—R : r : : 7 mm. : 3·1 mm.

Horizon and Locality.—Upper Silurian (Lower Ludlow) or Middle Silurian (Upper Wenlock); Hafod, Llandovery, Wales.

Genus **SCHUCHERTIA**, Gregory.

1858. *Palasterina*, Billings (part, not McCoy or Salter), Geol. Surv. Canada, Canad. Organic Rem., dec. iii, p. 76, pl. ix, fig. 1.
1862. *Palasterina*, Wright (part), Mon. Brit. Foss. Echinod., Oolitic, vol. ii (Mon. Pal. Soc., vol. for 1861), p. 26, fig. 16 *b*.
1899. *Schuchertia*, Gregory, Geol. Mag. [4], vol. vi, p. 351.
1900. *Trentonaster*, Stürtz, Verhandl. Naturh. Ver. preuss. Rheinl., Jahrg. 56, pp. 224, 225 (based on the same genoholotype as *Schuchertia*).
1914. *Schuchertia*, Schuchert, Fossilium Catalogus, Animalia, pt. 3, pp. 5, 8, 30, 38, 43.
1915. „ Schuchert, Bull. 88, U.S. Nat. Mus., pp. 51, 140, 152, 194, 195, 252.

Generic Characters.—See p. 205.

The genoholotype of *Schuchertia* is *S. stellata*, which was described more than fifty years ago by Billings as *Palasterina stellata*. The species is found in the Trenton (M. Ordovician) of Canada. Both Gregory and Stürtz, about 1899, recognised that the species was not a true *Palasterina*. Gregory gave the name *Schuchertia*. Stürtz, who published a little later, suggested the name *Trentonaster*.

In 1915 Schuchert described two new species, *S. laxata* and *S. ordinaria*, found respectively in the Upper Ordovician and basal Silurian of the United States. I am now able to show that *S. laxata* is found in the Upper Ordovician of Scotland, and that a fourth species, *S. wenlocki*, n. sp., occurs in the Middle Silurian of Scotland. This extends the range of the species both geographically and in horizon. It seems very probable, judging by the way the species succeed each other in the ascending order of the strata, that they are descendants of one another.

The oral surface of *Schuchertia* (Text-fig. 154, p. 216) may be derived from that of a form like *Eoactis*—(1) by the further differentiation of the infero-marginalia which brings about a superficial resemblance to the oral surface of *Hudsonaster*, (2) by an outgrowth of the interradial areas which carries the madreporite oralwards. The latter character we have learnt to associate with "*débris* feeding." The former character is probably associated with the flattening of the body, for which a cause is suggested by the progressive changes of the apical surface detailed below.

The apical surface of the earliest species, *S. stellata* (Text-fig. 149), is quite dissimilar from that of a *Hudsonaster*, and even at this early stage shows a general resemblance in its numerous columns, sometimes twisted, to the same surface of recent members of the Paxillosa (compare the text-figure with Verrill, 1914, pl. ciii, fig. 2, *Luidia foliolata*). Progressive changes heighten this resemblance and make it more exact. Schuchert noted that the apical plates in *S. stellata* were only

TEXT-FIG. 149.—Camera lucida drawing of the apical surface of *Schuchertia stellata* (after Schuchert). × 8.

tumid, while in a later species, *S. ordinaria*, they become spicular. The account given below of the latest form, *S. wenlocki*, shows that by the Middle Silurian very definite paxillæ have developed. The recent Paxillosa, as suggested by the name, are characterised by paxillæ, and a study of their mode of life suggests a physiological reason for their presence. The forms live, when at rest, just below the surface of the sand, and clearly might be expected to find some difficulty in respiration. Their breathing organs are papulæ, naked protruding patches of skin, which are found between the ossicles. The spines of the paxillæ act like an umbrella and keep the particles of sand away from the sensitive skin and loosen the sand, so as to allow the ready ingress of streams of freshly aërated water.

It is possible that the sunk valleys between the infero-marginalia of *S. wenlocki* (Text-fig. 124, p. 183) were occupied by specialised spines carrying cilia and so producing respiratory currents, exactly as Cuenot has shown to be the case in the recent *Astropecten* and *Luidia*. (These ridges on the infero-marginalia in *Astropecten* are shown in Text-fig. 141, p. 202.) We appear therefore to be able to trace progressive changes in *Schuchertia*, associated with a habit of retiring on occasion, if not altogether, beneath the surface of the bottom. It is probable that the animals did not go very deep. The recent *Luidia* when at rest is so near the surface that the respiratory currents form "star-like impressions agreeing with the starfish in size and form." The fragmentary condition in which *S. laxata* is found both in Europe and America (see p. 212) suggests that it could not have been deeply buried at death, but that slight current-action could displace the ossicles when no longer held together by living tissue.

The cross-section given (Text-fig. 145) shows that only infero-marginalia are present. We can interpret this as meaning either that supero-marginalia have been lost, as in the recent *Luidia*, or that like *Urasterella* (p. 130) the form has not yet acquired supero-marginalia. Schuchert takes the first view, and regards the general resemblance of the oral surface to that of *Hudsonaster* as being due to a descent from that Asteroid.

I do not think Schuchert is correct, for, apart from the possible descent of *Schuchertia* from a form similar to *Eoactis*, an examination of *S. stellata* does not show the markedly defined infero-marginalia characteristic of the later species, but a far greater resemblance to their less distinct appearance in *Urasterella*. It is the very prominent infero-marginalia, far more apparent in the later than in the earlier species, which make the form so very like *Hudsonaster*; and if the above argument be correct, the resemblance arises secondarily and is not a primitive character. Personally I should be inclined to assign the presence of the differentiated infero-marginalia to a progressive flattening of the body, which causes a sharp edge to the disc (see p. 202).

A progressive diminution in the comparative size of the adambulacralia is dealt with on p. 185.

An exceedingly interesting feature is the constancy in shape of the mouth-angle plates (Text-fig. 143, p. 203) throughout the life-history of the genus. They are long, narrow, and sharply bent at the junction of the oral and adoral surfaces. We shall see that *Palasterina* also has very characteristic mouth-angle plates recognisable through a considerable geological period.

As the species make so interesting a series, I give a full description whether or no they are known in British rocks. The following table gives their diagnostic characters:

S. stellata.—Small form with short arms. R equals in larger specimen 9 mm. and is approximately twice r. Adambulacralia about as broad as the infero-marginalia. Apical plates closely fitting and slightly tumid. Middle Ordovician.

S. laxata.—Larger form with longer arms. Apparently R may be over 30 mm. and nearly three times r. Adambulacralia as broad as the infero-marginalia. Apical plates rather irregular and slightly tumid. Upper Ordovician.

S. ordinaria.—Form imperfectly known. Apical plates more spicular. Basal Silurian.

S. wenlocki.—General form and size very similar to *S. laxata*. Adambulacralia much less prominent than the infero-marginalia. Apical plates have become paxillæ. Middle Silurian.

A madreporite has not been identified in specimens of the first three species. In *S. wenlocki* it is large and on the oral surface (Text-fig. 154, p. 216).

1. **Schuchertia stellata** (Billings). Plate XVI, fig. 8; Text-fig. 149.

1857. *Palasterina stellata*, Billings, Geol. Surv. Canada, Rep. Progress for 1853—1856, p. 209.
1858. „ „ Billings, Geol. Surv. Canada, Canad. Organic Rem., dec. iii, p. 76, pl. ix, figs. 1 *a*, 1 *b*.
1862. „ „ Wright, Mon. Brit. Foss. Echinoderm., Oolitic, vol. ii (Mon. Pal. Soc., vol. for 1861), pp. 26, 27, fig. 16 *b*.
1876. „ „ Quenstedt, Petrefaktenkunde Deutschlands, vol. iv, p. 74, pl. xcii, fig. 34.
1900. *Trentonaster stellata*, Stürtz, Verhandl. Naturh. Ver. preuss. Rheinl., Jahrg. 56, pp. 217, 224, 225.
1914. *Schuchertia stellata*, Schuchert, Fossilium Catalogus, Animalia, pt. 3, pp. 32, 43.
1915. „ „ Schuchert, Bull. 88, U.S. Nat. Mus., pp. 196—198, pl. xxxii, fig. 2; pl. xxxiii, fig. 1.

Material.—The holotype, which shows the oral surface, was found by E. Billings, and is preserved in the Canadian Geological Survey Collection (no. 1399) at Ottawa. A second specimen in the same collection shows the apical surface. It was found on Governor General Bay, near New Edinburgh, Canada.

Specific Characters.—See p. 210.

Description.—The following description is given by Schuchert:

"Abactinal area composed of a series of plates which are more or less closely adjoining, and on the rays are arranged in distinct but twisted columns. This twisting is due to the insertion of new columns of plates, always on the right side, crowding the older ones to the left. The plates on the rays are subquadrangular to elongate subquadrangular, increasing in size proximally, and on the disc are largest and generally subcircular in outline, or faintly stellate. The plates appear to be smooth. At the apex of the ray are two somewhat larger plates followed by three columns, and on each side of this there are two other columns of ossicles. Near the beginning of the interbrachial arcs the rays have from seven to eight columns of plates.

"Madreporite not distinguished among the abactinal plates.

"Actinally the most conspicuous columns are the adambulacrals bounding the very narrow ambulacral grooves. These ossicles are subquadrangular in outline near the base of the column, but become wider than long distally; there are about 15 in a column, terminating proximally in two larger, prominent, wedge-shaped plates of the oral armature. Interradially upon each pair of oral pieces is placed a large, single, pentagonal plate (holds the position of axillary interbrachials), against which rest two diverging inframarginal columns, each with 13 or 14 ossicles, and these columns continue adjoining the adambulacrals. Before attaining the distal ends of the rays they gradually become smaller and pass over to the abactinal side. Other actinal disc plates are also present, but apparently are arranged in quincunx, and are smooth like those of the abactinal side.

"Ambulacrals unknown."

Measurements.—The holotype gives R : r : : 6 mm. : 3 mm. The second specimen gives R : r : : 9 mm. : 4 mm.

Horizon and Locality.—Middle Ordovician (Trenton Limestone); Canada.

2. **Schuchertia laxata,** Schuchert. Plate XV, fig. 1; Text-figs. 150—153.

1914. *Schuchertia laxata,* Schuchert, Fossilium Catalogus, Animalia, pt. 3, p. 38.
1915. „ „ Schuchert, Bull. 88, U.S. Nat. Mus., pp. 198—9, pl. xxxii, fig. 3; pl. xxxiii, figs. 2, 3.

Material.—Four moulds in Mrs. Gray's Collection from the Starfish Bed of Thraive Glen (nos. D. 283, D. 330—D. 332), all fragmentary. D. 283 shows a portion of the apical surface of an arm. The apical ossicles have fallen away, exposing the ambulacralia (Text-fig. 126, p. 186). D. 330 shows the apical surface

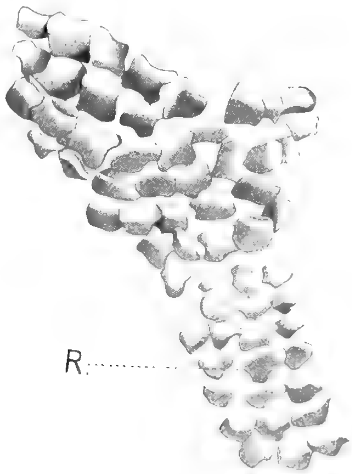
TEXT-FIG. 150.—Apical plates of *Schuchertia laxata* (after Schuchert). × 8.

of a portion of two arms and is figured Pl. XV, fig. 1, and Text-fig. 151. Views of portions of the oral surface are given by D. 331 and D. 332. The plates are much displaced in the former specimen. The latter shows only portions of two arms but they are in good condition.

Schuchert notes that in America "six specimens are known, four of which are poorly preserved and but a jumble of plates. The specific name is given to indicate the generally separated condition of the plates." The British material repeats this condition.

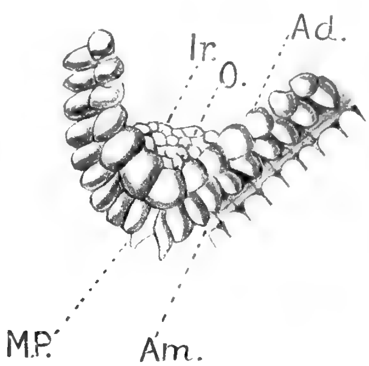
Specific Characters.—See p. 211.

Oral Surface (Text-figs. 152, 153).—For comparison with the British specimens I have reproduced Schuchert's original figure, in which both the odontophor and the proximal infero-marginalia are very distinct. The mouth-angle plates are



TEXT-FIG. 151.—Drawing of a portion of the apical surface of *Schuchertia laxata?* *R.*, radialia. × 6.

drawn with a wide gape, and are apparently preserved much in the same position as they are in the specimen of *S. wenlocki*, figured Pl. XV, fig. 3. D. 331 shows a pair of similar mouth-angle plates, but here the muscle occupying the gape had contracted before death, and the gape is scarcely visible. The odontophor is as in the American specimen. The interradial area in the American specimen is

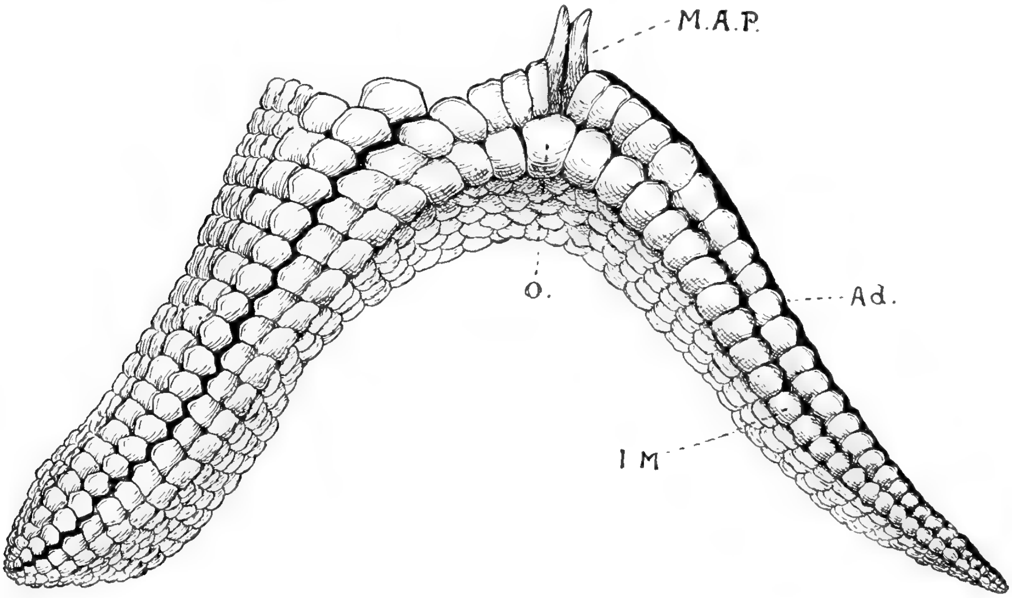


TEXT-FIG. 152.—An interradial area and the ambulacral groove of *Schuchertia laxata* (after Schuchert). *Ad.*, adambulacral; *Am.*, ambulacral; *Ir.*, interradial plates; *M.P.*, mouth-angle plate; *O.*, odontophor. × 4.

occupied by numerous small plates described by Schuchert as "smallest in the inner axillary areas and thence increasing rapidly to a size maintained throughout the interbrachial areas. In form they are either diamond-shaped or subquadrate, centrally tumid, and each plate seems to have borne one central and two or three lateral spines." D. 332 shows similar plates perhaps just a little larger than in the American figured specimen. They merge gradually into the apical skeleton.

Schuchert's drawing shows the adambulacralia not meeting above the radial line. In D. 331 and D. 332 the adambulacralia meet across this line and completely close the groove. This may be simply due to a greater contraction of the walls of the groove at the time of entombment, or it may have some slight specific value (see below). The adambulacralia of the American species are said to be very convex. Those of the British form are rounded but not strikingly convex. The inner sides of the adambulacralia are stated by Schuchert to bear tufts of short blunt spines.

Apical Surface (Pl. XV, fig. 1; Text-figs. 150, 151).—The American form has "abactinal areas of rays and disc composed of very numerous, small but irregularly sized, sub-quadrate or diamond shaped, slightly pustulose plates. The



TEXT-FIG. 153.—Line-drawing of *Schuchertia laxata* (combined from D. 331 and D. 332). *Ad.*, adambulacralia; *I.M.*, infero-marginalia; *M.A.P.*, mouth-angle plates; *O.*, odontophor. × 5.

arrangement is mainly in quincunx, but a columnar arrangement is also noticeable." Isolated plates of this form are shown in Text-fig 150. The drawing of the British form given, Text-fig. 151, is very good evidence of the identity of the two sets of material. The ossicles are distinctly more irregular than those of *S. stellata*. The distal portion of the arm in the drawing shows only three rows of plates. At least two more were undoubtedly present originally, but are now represented only by scattered plates. The median row shows a tendency to differentiate into breast-plate-shaped radialia.

Measurements.—D. 332 gives the following approximate measurements: R : r : : 17 mm. : 6 mm. The other specimens were probably of approximately the same size.

Schuchert states that the best American specimen "measures: R = 18 mm., r = 6 mm., R = 3 r. The University of Chicago individual : R = 23 mm., r = about 8 mm., R = 2·8 r. Other specimens indicate a growth twice as long as the former one."

Horizon and Locality.—Upper Ordovician (Ashgillian); Girvan, Ayrshire, Scotland. The American species is from the Upper Ordovician (Richmond Formation) of Ohio.

3. **Schuchertia ordinaria,** Schuchert.

1915. *Schuchertia ordinaria,* Schuchert, Bull. 88, U.S. Nat. Mus., p. 199 (not figured).

Material.—One specimen in the Gurley Collection of the University of Chicago (no. 10992). Schuchert remarks—"The specimen cannot be freed of the adhering clay sufficiently to make an instructive photograph, and is therefore not illustrated."

Specific Characters.—See p. 211.

Description.—"The species is most closely related to *S. laxata*, but is smaller and with a comparatively larger disc. Therefore the rays do not protrude beyond the disc so far as in the latter form. Abactinal skeleton consists of minute tumid ossicles that are more cut along their edges than in *S. laxata* and therefore more spicular" (Schuchert, *loc. cit.* p. 199).

Measurements.—R = 11 mm, r = about 6·3 mm.

Horizon and Locality.—The basal Silurian Girardeau Limestone ; Alexander County, Illinois, U.S.A.

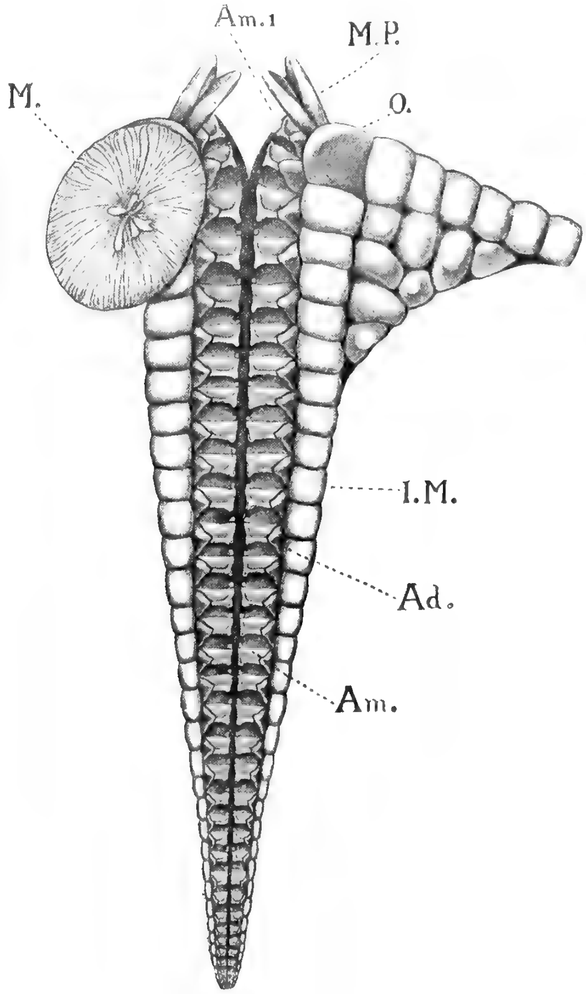
4. **Schuchertia wenlocki,** n. sp. Plate XIV, figs. 5, 6; Plate XV, figs. 2–4; Text-figures 124 (p. 183), 127 (p. 187), 143 (p. 203), 145 (p. 204), 154—156.

1916. *Schuchertia,* n. sp., Spencer, British Palæoz. Asterozoa (Mon. Pal. Soc., vol. for 1915), p. 67.

Material.—Eleven specimens of the species are known, all moulds in sandstone from the Starfish Bed of Gutterford Burn. They are in the Royal Scottish Museum (nos. 1897, 32/475, 477, 478, 480, 482, 484, 485, 486, 487, 490, 491). Specimen no. 485, a cast of which is photographed in Pl. XIV, fig. 5, is taken as the holotype of the species.

Specific Characters.—See p. 211.

Oral Surface (Pl. XIV, figs. 5, 6; Pl. XV, figs. 2, 3; Text-fig. 154).—Excellent oral views can be obtained from casts of 475, 484, 485, which show almost the whole of the original specimens. Casts from 486, 487 and 491 show the same surface but are more fragmentary. The reconstruction (Text-fig. 154), is based mostly on a cast from 485, although details are added from other material. The odontophor is a very prominent flat plate, shaped somewhat like a kite. Its proximal edges are convex and its distal edges slightly concave. Each proximal edge carries a mouth-angle plate and two adambulacralia. The mouth-angle plates are high, narrow, and project well into the mouth-cavity (see Text-fig. 143, p. 203). Proximally the triangular depression for the inter-dental muscle shows as a deep depression. If this muscle be relaxed, as in some

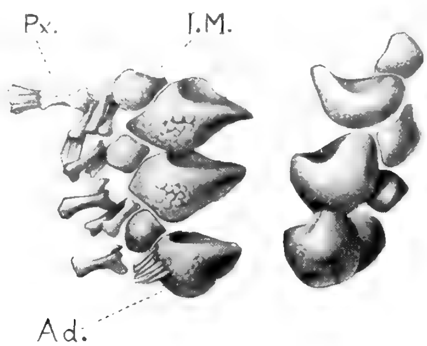


TEXT-FIG. 154.—Slightly reconstructed view of an arm and a portion of the disc of *Schuchertia wenlocki*. *Ad.*, adambulacral; *Am.*, ambulacral; *I.M.*, infero-marginal; *M.*, madreporite; *M.P.*, mouth-angle plate; *O.*, odontophor. × 6.

specimens, the mouth-angle plates appear strongly divergent (Pl. XV, fig. 3). A fringe of slender spines projects from the mouth-angle plate into the mouth-cavity. The first two pairs of ambulacralia are small. By inference we may suppose that the proximal tube-feet were also small.

These proximal pairs of ambulacralia do not meet across the middle line but form divergent arms of a V. The first two pairs of adambulacralia are also smaller than the immediately succeeding ossicles, which are almost constant in size for some distance along the arm. In consequence the proximal region of the arm is straight, not petaloid as in *Palasterina* (see below, p. 225).

The proximal infero-marginalia are broader than long, with a weakly concave upper surface (Text-fig. 124, p. 183). About a third of the way down the arm they become longer than broad and much more swollen. Finally they become almost globular and pass over to the apical surface. Text-fig. 155 shows these small, globular infero-marginalia clearly distinguishable from the apical paxillæ. I have made a suggestion above (p. 209) that some of the infero-marginalia may have been modified for respiratory purposes. The infero-marginalia are approximately equal in number and more or less alternate with the adambulacralia—characters which appear to be constant in the genus. The interradial plates of the disc are not arranged in a constant manner and also vary in number. They are polygonal, with distinctly swollen central areas.



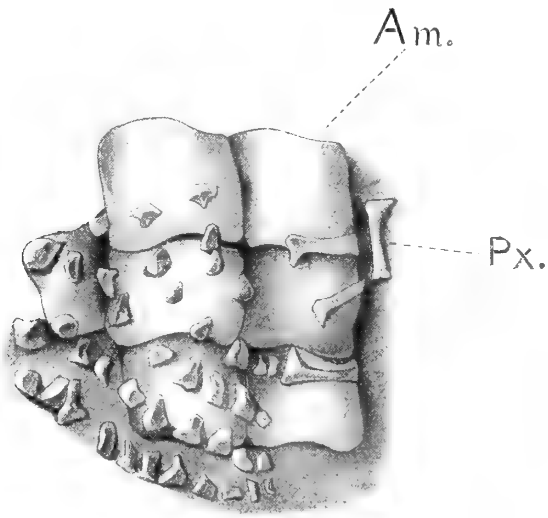
TEXT-FIG. 155.—Wash-drawing of the end of an arm of *Schuchertia wenlocki*. *Ad.*, adambulacral; *I.M.*, infero-marginal; *Px.*, paxilla displaced from apical surface. × 30.

The madreporite is a large oval plate seen in all the three more perfect specimens. It overlaps the other plates of the interradial area, suggesting, as in *Palasterina primæva* (p. 223), that it was embedded in a skin which covered the interradial ossicles. Details of the minute structure of the groove have already been given (p. 182).

Apical Surface (Pl. XV, fig. 4; Text-figs. 127 and 156).—It is extremely difficult to get a really good view of the apical covering, as the plates are usually much displaced. The arrangement of the ossicles can only be seen in a rather indistinct specimen (no. 490). Casts from this and other specimens (nos. 477, 478, 480, 482) show that the apical covering was composed of numerous small plates, arranged in rows but not showing differentiation into radialia, adradialia and supero-marginalia. Favourable views of the plates show them to be paxilliform (see Text-fig. 145, p. 204, and Text-fig. 156, p. 218). Each paxilla possesses a flat top, a long shaft and a spreading base. Spines can be distinguished on some of the paxillæ in specially good casts.

It is extremely difficult to get a good cast of a paxilla unless it is end on, for the air inside a vertical hollow in the mould has no method of escape and so keeps the rubber out (*cf.* p. 151). If the holes are at an angle the rubber enters more readily.

Oral Surface (Text-fig. 120).—The displacement of the apical covering, alluded to above, allows one to obtain good views of the ossicles of the oral surface as seen



TEXT-FIG. 156.—Apical view of a portion of the arm of *Schuchertia wenlocki*. *Am.*, ambulacral; *Px.*, paxilla. × 12.

from above. Text-fig. 127 (p. 187) gives such a view in the region of the mouth. The odontophor is almost flat, but one can see a suggestion of the **Y** so conspicuous in *Stellaster*. The arrangement of the proximal ambulacralia is somewhat as in the Platanasteridæ (p. 177). The first ambulacral is small. Although it is displaced it is seen, like the second ambulacral, to lie on one edge. Neither of these ossicles meets its pair across the median line of the arm. The more distal ambulacralia have slightly advanced in structure from those of the Ordovician species (Text-fig. 126, p. 186). The longitudinal muscle-depressions are well marked, and there is a distinct beginning of a ball and socket. The inner edges of the plates are slightly raised for the attachment of the dorsal transverse muscles.

Measurements.—Specimen no. 490—R : r : : 21 mm. : 6·5 mm. Specimen no. 485—R : r : : 20 mm. : 7 mm.

Horizon and Locality.—Wenlockian (the Starfish Bed); Gutterford Burn, Pentland Hills.

Genus **PALASTERINA**, McCoy.

1848. *Uraster*, Forbes (pars), Mem. Geol. Surv. Gt. Brit., vol. ii, pt. ii, p. 463.
1849. „ Forbes (pars), Mem. Geol. Surv. United Kingdom, dec. i, p. 2.
1851. *Palasterina*, McCoy, Brit. Palæoz. Foss., p. 59.
1857. „ Salter, Ann. Mag. Nat. Hist. [2], vol. xx, pp. 324, 327.
1858. „ Billings (pars), Canad. Organic Rem., vol. iii, p. 76.
1859. „ Salter (pars), in Murchison, Siluria, 3rd edit., p. 248.
1879. „ Zittel, Handb. Palæont., vol. i, p. 453.
1884. „ La Touche (pars), Handb. Geol. Shropshire, p. 34.
1890. *Palasterina*, Stürtz (pars), Palæontographica, vol. xxvi, p. 246.
1893. „ Stürtz (pars), Verhandl. Naturh. Ver. preuss. Rheinl., Jahrg. 50, pp. 43, 60.
1899. *Palæasterina*, Gregory, Geol. Mag. [4], vol. vi, p. 349.
1899. *Lindstromaster*, Gregory, *loc. cit.*, [4], vol. vi, pp. 344, 346.
1900. *Hisingeraster*, Stürtz, Verhandl. Naturh. Ver. preuss. Rheinl., Jahrg. 56, pp. 224, 225.
1900. *Pseudopalasterina*, Stürtz, *loc. cit.*, Jahrg. 56, pp. 219, 224.
1910. *Palasterina*, Schöndorf, Jahrb. Nassau. Ver. Naturk., vol. lxiii, p. 220.
1914. „ Schuchert, Fossilium Catalogus, Animalia, pt. 3, pp. 5, 7, 29, 30.
1914. *Lindströmaster*, Schuchert, *loc. cit.*, pt. 3, pp. 5, 7, 21, 23.
1914. *Pseudopalasterina*, Schuchert, *loc. cit.*, pt. 3, pp. 5, 7, 36.
1915. *Palasterina*, Schuchert, Bull. 88, U.S. Nat. Mus., pp. 49, 130, 138, 140, 150, 154, 156, 196.
1915. *Lindströmaster*, Schuchert, *loc. cit.*, pp. 138, 140, 148, 154, 156.
1915. *Pseudopalasterina*, Schuchert, *loc. cit.*, pp. 138, 156.
1915. *Lindstromaster*, Bather, Geol. Mag. [6], vol. ii, p. 318.

Generic Characters.—Groove with an open ambulacral channel. Bases of arms separated by strongly calcified disc area. Mouth-angle plates swollen with rounded sides. Odontophor in adult either absent or recognisable with difficulty. Adambulacralia bound the oral surface of the arm, and frequently have a ridge bearing stout spines (see p. 205).

The name *Palasterina* was suggested by McCoy, who in 1851 (when writing about the three species named by Forbes *Uraster ruthveni*, *U. hirudo* and *U. primævus*) stated: "Before I was aware Professor Forbes had described them, it seemed to me that the *U. ruthveni* and *U. hirudo*, as well as the similar American species *Urasterella pulchella*, might be easily separated from the great starfishes forming the recent genus *Uraster* by their small size and much more simple skeletons, and I had named the genus *Urasterella* in my manuscript. The *U. primævus* I thought generically distinct from the other two, as the rays were not contracted at base, etc.; and I had named it *Palasterina*, from its resemblance to the recent genus *Asterina*." McCoy then went on to publish the descriptions given by Forbes.

Salter in 1857 definitely accepted McCoy's name with the same genotype, *P. primæva*. He defines the genus as follows: "Pentagonal, depressed, the arms a little produced, with three or five principal rows of tubercles above, combined with a plated disc which fills up the angles; ambulacra rather shallow, of subquadrate or slightly transverse ossicles, bordered by a single row of squarish large plates, the lowest of which (ad-oral adambulacral plates, Huxley; angle ossicula, Forbes) are large and triangular, bearing combs of spines (Upper Silurian)."

Unfortunately the specimen examined and described by Salter was not *P. primæva*, but the form described later by Gregory as "*P. bonneyi*." Neither Gregory nor later authors appear to have noticed this, and in consequence there has been some confusion.

I have placed in the genus several forms which some previous observers have separated rather widely. These include "*Lindstromaster*" *antiquus*, Hisinger, from the Wenlock (Middle Silurian) of Gotland, *P. primæva*, Forbes, and "*P. bonneyi*" from the Ludlow (Upper Silurian) of England, and "*Pseudopalasterina*" *follmanni*, Stürtz, from the Bundenbach (Lower Devonian) of Germany. I am also able to describe a little new material from the Wenlock horizon of both England and Scotland. All these forms possess one characteristic type of mouth-angle plate (Text-fig. 144, p. 203), and agree in the rounded shape of the arm and other general characters.

The new form from the Wenlock of Scotland appears to be a young specimen. In many respects, particularly in the shape of its odontophor, it recalls *Eoactis* (see p. 205).

For the reasons stated below I think that we can limit the species as follows:

(1) A Wenlock species, *P. antiqua*, Hisinger, present also in the Ludlow Beds and passing directly into—

(2) The Devonian *P. follmanni*, Stürtz.

(3) A Ludlow species, *P. primæva*, Forbes, which seems to be characteristic of its own horizon and locality (passage beds between Lower and Upper Ludlow in Lake District).

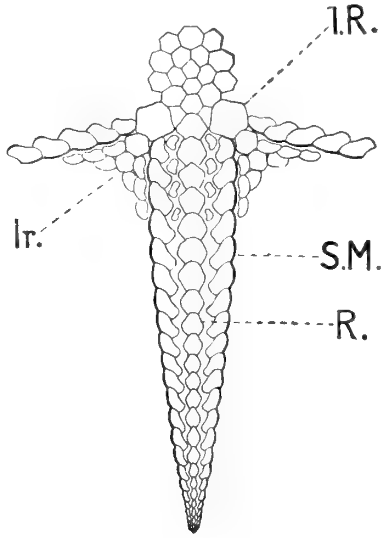
The following table gives the diagnostic characters of these species:

P. primæva.—Form of medium size; R may be 18 mm. A comparatively small number of ossicles in the interradii. Radialia and marginalia can be identified.

P. antiqua.—Form of medium size; R may be 17 mm. A large number of ossicles in the interradii. Radialia and marginalia can be identified.

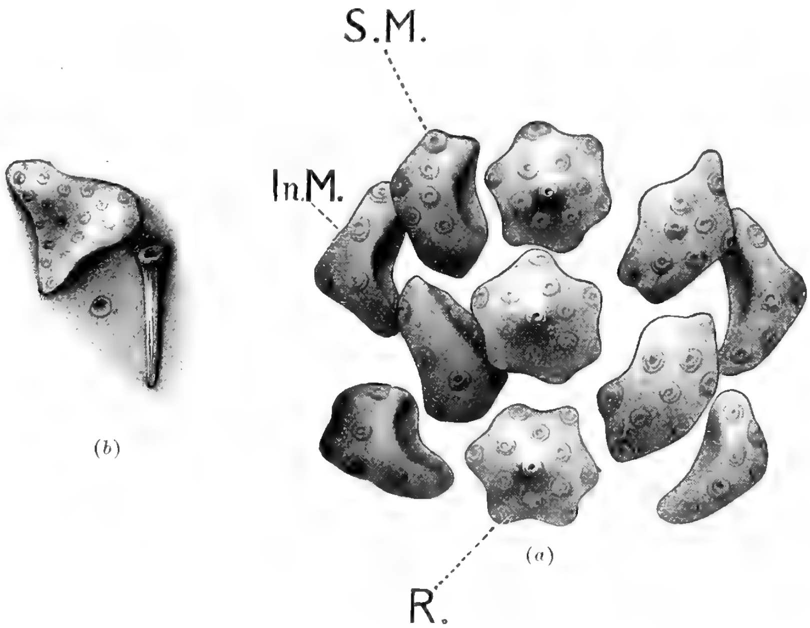
P. follmanni.—Large form; R may be 113 mm. Arm much swollen with numerous similar rows of apical ossicles, which may be squeezed by post-mortem distortion into oral surface forming large interradii.

The characters of the apical surface can be understood most clearly if we commence with a study of *P. primæva*. In this form both radialia and marginalia are differentiated (Text-fig. 146, p. 204, and Text-fig. 157). The earlier observers, who had not noted the oral position of the madreporite, classified the form, in consequence, among the Phanerozonate Asteroidea. The apical



TEXT-FIG. 157.—Plan of ossicles on the apical surface of *Palasterina primæva*. *I.R.*, primary interradial; *Ir.*, intermarginalia; *R.*, radial; *S.M.*, supero-marginal. × 5.

plates are covered with pustules, which are shown slightly exaggerated in Text-fig. 158.



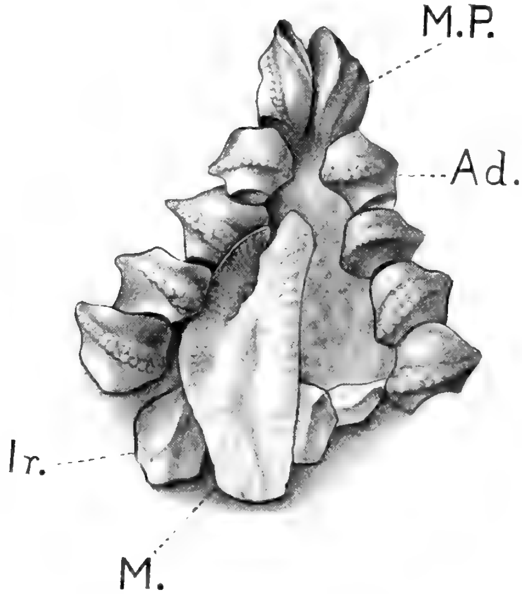
TEXT-FIG. 158.—(*a*) Wash-drawing of ossicles across the apical surface of a somewhat compressed specimen of *Palasterina primæva*. *In.M.*, infero-marginal; *R.*, radial; *S.M.*, supero-marginal. × 30. (*b*) On left an isolated ossicle with detached spine from a specimen of *P. antiqua* (Brit. Mus. no. 40301).

The faint ornament suggests that the spines fitting on these pustules were slender and easily destroyed, and they are usually missing in the specimens. If present there is only one to a plate (Text-fig. 158 *b*), and one may surmise that this was

30

a central spine stouter than the remainder. This ornament must have been very similar to that in *Palæosolaster* (p. 239). The arm in *P. follmanni* shows no differentiation of marginalia. It was clearly more rounded and flexible (Pl. XVI). The position of the arms in Pl. XVI, figs. 6, 7, proves that they had the power of bending upwards over the disc. Fig. 6 shows only the base of the arms in oral view. The other side of the specimen has been cleared of the matrix and shows the remaining portions of the arms folded over the disc. The upward flexure is very clear in the specimen photographed in fig. 7.

The fact that the arms are preserved in this condition, and the general good state of preservation of the specimens, suggest to me that the form lived buried in the mud with the tips of its arms flexed and searching for food at the surface of

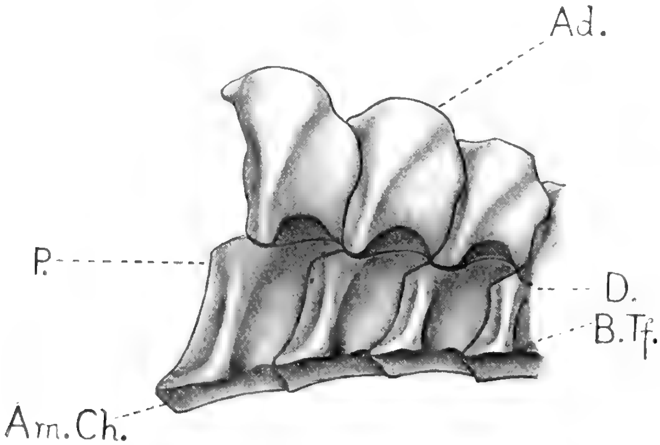


Text-fig. 159.—Wash-drawing of an angle of the disc of *Palasterina primæva* (from Sedgwick Mus.). *Ad.*, adambulacral; *Ir.*, interradial plate; *M.*, madreporite; *M.P.*, mouth-angle plate. × 15.

the bottom. In this respect it contrasts with *Schuchertia*, which appears to have lived near the surface (p. 210).

The constitution of the oral surface is most typically shown in *P. primæva* (Text-fig. 161, p. 225). The greater part of the surface is formed by the prominent adambulacralia. The oral interradii in the various species, and even in individual specimens, vary considerably in extent. Those of *P. primæva* usually contain but a few plates. In both *P. follmanni* and *P. antiqua* these areas may be quite extensive (see, *e.g.*, Text-fig. 165, p. 229, and Text-fig. 168, p. 232). The photographs on Pl. XVI give the explanation of these discrepancies. When the arms are high and the body swollen, post-mortem compression may cause the extensive lateral surfaces in the interradii to be forced oralwards and so make the form look as if it had a large flat disc.

The madreporite is a large thin plate. It presents features which I do not understand. Text-fig. 159 has an appearance which suggests that it is embedded in a membrane overlying the interradial plates. Its inner proximal surface over-rides the adambulacralia in an obviously unnatural position. The whole appearance indicates that the madreporite overlaid a large vesicle which projected oralwards and collapsed after death. The thin madreporite was forced down on to the adambulacralia and became slightly fractured during this process.



TEXT-FIG. 160.—Wash-drawing of the floor and inner wall of the ambulacral groove of *Palasterina primæva* (from Sedgwick Mus.). *Ad.*, adambulacral; *Am.Ch.*, ambulacral channel; *B.Tf.*, channel for the branch of the radial water-vascular canal to the tube-foot; *P.*, proximal direction; *D.*, distal direction. × 30.

The simple flooring-plate character of the ambulacralia is shown in Text-fig. 160. The same ossicles in apical view are shown in Text-fig. 164, p. 227. The ambulacralia near the mouth are but little differentiated (Text-fig. 163, p. 227).

1. **Palasterina primæva** (Forbes). Plate XV, figs. 5—7; Plate XVII, fig. 3; Text-figs. 30 (p. 37), 138 (p. 195), 157—164.

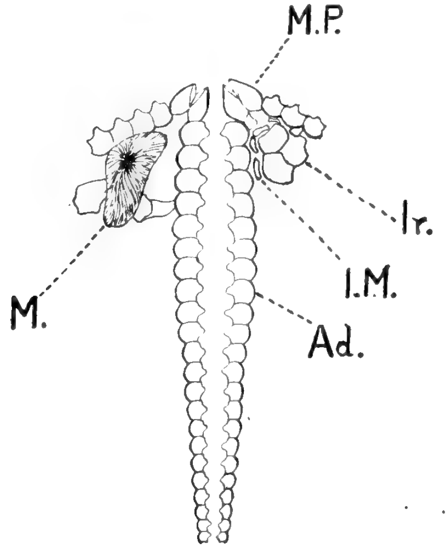
1848. *Uraster primævus*, Forbes, Mem. Geol. Surv. Gt. Brit., vol. ii, pt. 2, p. 463.
1849. „ „ Forbes, Mem. Geol. Surv. United Kingdom, dec. i, p. 2, pl. i, figs. 2 *a*, 2 *b*.
1851. „ „ Forbes in McCoy, Brit. Palæoz. Foss., p. 60.
1851. *Palasterina primæva*, McCoy, *loc. cit.*, p. 59.
1854. *Uraster primævus*, Murchison, Siluria, p. 221, fig. 39.
1876. „ „ Quenstedt, Petrefakt. Deutschl., 1, iv, p. 74, pl. xcii, fig. 35.
1893. *Palasterina primæva*, Stürtz, Verhandl. Naturhist. Ver. preuss. Rheinl., Jahrg. 50, p. 44.
1899. „ „ Stürtz, *loc. cit.*, Jahrg. 56, pp. 214, 224.
1899. *Palæasterina primæva*, Gregory, Geol. Mag. [4], vol. vi, p. 349.
1910. *Palasterina primæva*, Schöndorf, Jahrb. Nassau. Ver. Naturk., vol. lxiii, pp. 220, 243, 250.
1913. *Palæasterina primæva*, Spencer, Introductory Section to this Monograph, pp. 37, 38, Text-fig. 30.
1914. *Palasterina primæva*, Schuchert, Fossilium Catalogus, Animalia, pt. 3, pp. 31, 44.
1915. „ „ Schuchert, Bull. 88, U.S. Nat. Mus., pp. 149, 151, 152, 153.

Material.—There are many specimens in various museums, nearly all impressions in sandstone. Individuals are often crowded together on the same slab, suggesting that, like many Ophiuroidea, the form occurred in swarms. The most extensive collection is in the Sedgwick Museum, Cambridge, where there are twelve slabs, with another slab which contains two impressions associated with *Urasterella ruthveni* (see p. 140). Six of the slabs are stated to be from the Bannisdale Slates, High Thorns, Underbarrow, and are registered as *a*/517. A note is attached to the label that Forbes' original figures were based on this material. I have identified one of the impressions (slab *d*) as giving the cast from which Forbes' fig. 2 *a* was drawn, but I cannot recognise the original of fig. 2 *b*. The specimen on slab *d* is therefore hereby selected as the holotype of the species. It is figured here, Pl. XV, fig. 5. Four of the slabs (*f*, *g*, *h*, *k*) are labelled Bannisdale Slates, nr. Kendal, and a note is attached that these were in a Kirkby Lonsdale drawer unlabelled. The other two slabs are from the Bannisdale Slates, High Thorns (no. 146*), and from Bannisdale Slates (?), Underbarrow (no. 48), respectively. The British Museum (Nat. Hist.) has specimens registered as E. 61, E. 4990—4993, all from Underbarrow. Specimens in the Museum of Practical Geology, Jermyn St., are registered as 25349, 25350 and 25375. The locality of the first is near Kendal, the other two are from Underbarrow. The following specimens are in the Kendal Museum: no. 9 from the "Asterias bed," Bannisdale Slates, Underbarrow; nos. 7, 34, from the Bannisdale Slates, High Thorns, Underbarrow. It seems clear that all the specimens are from the same horizon and locality (see also p. 142).

Specific Characters.—See p. 220.

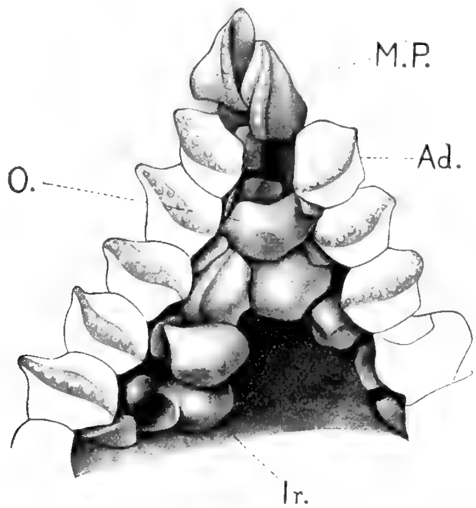
Oral Surface (Pl. XV, fig. 7; Text-figs. 161, 162).—The adambulacralia are very prominent indeed, and it is their shape and disposition which give the arm its distinctive appearance. They margin the arm, and the largest lie about the base of the free portion of the arm, with the result that it has a distinctly petaloid appearance.

Each adambulacral has a characteristic shape. It only meets its neighbours along a comparatively slender articulation (Text-fig. 162). The surface above the line of contact is much swollen. The nose, which is, as usual, on the proximal portion of the ossicle, is continued into a ridge, which at first starts backwards, and then runs along the middle of the ossicle. The ridge possesses pustular elevations which carried long spines. Text-fig. 160, p. 223, gives a view of the ossicle of the groove as seen from within (corresponding to the aspects figured Text-figs. 124, 125, pp. 183, 184). The adambulacralia look as if they were tipped away from the mouth. This is due to slight distortion in the rubber cast from which the drawing was made. Really they tip, as is usual, towards the mouth. The groove is deep, and the adambulacralia form a steep wall just as in *Urasterella* (see p. 133). The ambulacralia have the same general character as those of *Schuchertia* (Text-fig. 124, p. 183). The median ridge as figured appears to be thicker and more rounded than in *Schuchertia*, but the ossicles on the other side of the groove of the same arm as figured show a thin ridge.



TEXT-FIG. 161.—Plan of the ossicles on the oral surface of *Palasterina primæva*. *Ad.*, adambulacra *I.M.*, infero-marginal; *Ir.*, interradial plate; *M.*, madreporite; *M.P.*, mouth-angle plate. × 5.

A very good view of the groove in the region of the mouth was obtained by bending rubber casts of specimen *k* from the Sedgwick Museum while still



TEXT-FIG. 162.—Wash-drawing of an angle of the disc of *Palasterina primæva* (from Sedgwick Mus.). Lettering as in Text-fig. 159. *O*, plate which corresponds in position with the odontophor of related species. × 12.

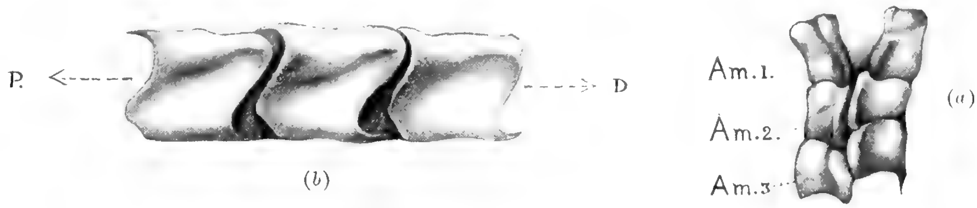
soft. The groove was thus forced open with but little distortion of the ossicles (Text-fig. 138, p. 195). The mouth-angle plate is large. On its inner side it is hollowed to lodge the first tube-foot. There is a distinct apophysis. Between the apophysis and the oral surface of the plate runs the groove for the nerve-ring. Behind the apophysis is the groove for the circular water-vascular ring. The hollow for the fitting of the first adambulacral is also shown. It is rather larger in the drawing than in reality because of the slight distortion of the cast. The great general resemblance between this mouth-angle plate and the same plate in a recent Asteroid has already been remarked (p. 196).

The first ambulacral has moved a little from its exact fitting on to the mouth-angle plate. The fitting shows that a peg-and-socket joint ensures a firm fitting of the two ossicles.

The mouth-angle plates in full oral view (Text-fig. 162) present a very characteristic appearance. They are much swollen, and divided almost throughout their length by a distinct deep triangular cleft bordered by two thin ornamented ridges. This same drawing also shows the interradial ossicles. One long ossicle, which may represent the odontophor, occupies the whole space between the second adambulacralia of neighbouring arms. Proximal to this ossicle are two smaller ossicles, and behind it four ossicles of various sizes. All these ossicles have swollen surfaces and appear to imbricate in the direction of the mouth. There appears to be some variation on this arrangement in the various specimens, possibly due to the degree of compression to which the form has been subjected. It is evident that increased compression would result in an apparent increase of the interradial areas due to a forcing downwards of a portion of the apical surface.

The madreporite is very large. As shown in Text-fig. 159, p. 222, it may overlie other interradial plates. The plate figured has slightly split in its anterior region, and the split shows that the plate is very thin. It is possible that it was also slightly flexible. Specimen no. 25349 shows the madreporite sticking close to the curve of the interradial region. The direction of the grooves on the madreporite suggests that the opening of the pore canal was at the edge of the disc—that is, in the primitive Ophiuroid position (see pp. 37, 181).

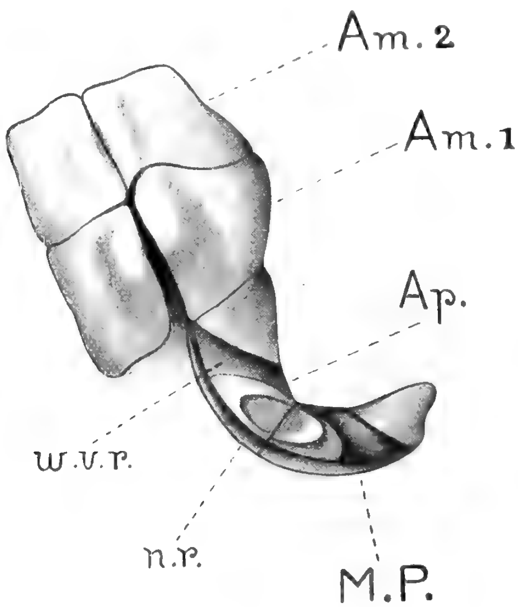
Apical Surface (Pl. XV, figs. 5, 6; Text-figs. 157, 158, 163, 164).—The arrangement of the ossicles is seen very clearly in casts from two impressions in the Sedgwick Museum (48 and *a*/517 A). The plan given (Text-fig. 157, p. 221) is drawn from these two specimens. It is strongly reminiscent of that met with in *Mesopalæaster primus* (Text-fig. 46, p. 86). The centre of the disc is occupied by a number of small plates, arranged approximately in two circles. Outside this is a circle of ten plates, five primary radialia and five primary interradialia. The primary interradialia are a little larger than the primary radialia. As stated above, the madreporite is not associated with a primary interradial as in the true Asteroidea, but is oral in position. Distal (and oral) to the primary interradialia are a number of plates (*Ir.*) occupying the same position as do the intermarginalia in *Mesopalæaster*. The radialia are hexagonal plates alternating in the proximal region of the arm with the supero-marginalia, and separated from these latter plates at the very base of the arm by a few adradialia. Just below the supero-marginalia, and except in compressed specimens only showing in side view, are two rows of distinct large plates (infero-marginalia), which are again succeeded by the small accessory plates (only seen in side or oral view). A drawing is given (Text-fig. 158, p. 221) to show the shape and ornament of these plates. The supero-marginalia overlap and are what I have called "bent finger" shaped. The series outer to



TEXT-FIG. 163.—(*a*) On right. Wash-drawing of the apical surface of the proximal ambulacralia of *Palasterina primæva* (from Sedgwick Mus.). *Am.*₁, first ambulacral; *Am.*₂, second ambulacral; *Am.*₃, third ambulacral. × 10. (*b*) On left. Lateral view of apical surface of adambulacralia. *P.*, proximal; *D.*, distal direction. × 18.

this are very similar. If seen in position in side view they appear **V**-shaped. Probably the shapes of both series may be derived from what I have called the half-moon shape in the case of *Uranaster* (see p. 110).

The ornament on the plates is very distinct from that of *Schuchertia*. On each ossicle is a central eminence which carried a long spine. Small pustules, which



TEXT-FIG. 164.—Adoral view of the mouth-frame of *Palasterina primæva* (from Sedgwick Mus., no. 344). *Am.*₁, ₂, first and second ambulacralia; *Ap.*, apophysis; *M.P.*, mouth-angle plate; *n.r.*, groove for nerve ring; *w.v.r.*, groove for water-vascular ring. × 18.

doubtless carried small spines, are scattered around this. A somewhat similar ornament is figured by Schuchert for *Promopalæaster bellulus* and *P. spinulosus* (1915, pl. xv, fig. 7; pl. xviii, fig. 8).

Several specimens have the apical covering displaced and show the upper surface of the ambulacralia. Text-fig. 163 gives such a view in the region of the mouth. The first ambulacralia are somewhat long and touch only at their distal ends. Each of the succeeding ossicles has a high median ridge (for the attachment of the dorsal transverse muscle) and a lateral swelling. The line of junction of successive ossicles is very close, and it appears as if the dorsal longitudinal muscles were of small importance.

An excellent apical view of the mouth-frame (Text-fig. 164) was obtained by dissolving an embedded calcite specimen and taking casts as the process proceeded. The arrangement of the various exposed parts is exactly as in Text-fig. 133, p. 191, except that (*a*) the first ambulacralia do not dip so steeply, and (*b*) the basal portion of the mouth-angle plate does not project so far into the mouth-cavity, (*c*) the interradial faces of the apophyses show depressions for the adductor muscles, but the adradial faces are smooth, suggesting that abductor muscles were absent (see p. 192).

Measurements.—The species varies in size between the following limits: largest specimen on slab *a*, Sedgwick Museum, R : r :: 18 mm. : 5 mm.; smallest specimen on slab *a*, Sedgwick Museum, R : r :: 8 mm. : 3 mm.

Horizon and Locality.—Upper Silurian (Ludlow); Westmoreland.

2. **Palasterina antiqua** (Hisinger). Plate IV, fig. 6; Plate XV, fig. 9; Plate XVI, figs. 1, 2; Text-figs. 165—170.

1837. *Asterias antiqua*, Hisinger, Lethea Suecica, p. 89, pl. xxvi, fig. 6.
1857. *Palasterina primævus*, Salter, Ann. Mag. Nat. Hist. [2], vol. xx, p. 327, pl. ix, figs. 2 *a*—*c*.
1862. „ „ Wright, Mon. Brit. Foss. Echin., Oolitic, vol. ii, pt. 1 (Palæontogr. Soc. for 1861), p. 26, fig. 16 *a*.
1899. *Lindstromaster antiqua*, Gregory, Geol. Mag. [4], vol. vi, pp. 343, 347, pl. xvi, figs. 1 *a*, 1 *b*.
1899. *Palasterina bonneyi*, Gregory, *loc. cit.* [4], vol. vi, pp. 349, 350, pl. xvi, figs. 2 *a*, *b*; text-figs. 1—3.
1910. *Lindströmaster antiqua*, Schöndorf, Jahrb. Nassauisch. Ver. Naturk., Wiesbaden, vol. lxiii, p. 225.
1910. *Palasterina bonneyi*, Schöndorf, *loc. cit.*, vol. lxiii, pp. 223, 250.
1914. *Lindströmaster antiquus*, Schuchert, Fossilium Catalogus, Animalia, pt. 3, p. 23.
1914. *Palasterina bonneyi*, Schuchert, *loc. cit.*, Animalia, pt. 3, p. 31.
1915. *Lindströmaster antiquus*, Schuchert, Bull. 88, U.S. Nat. Mus., pp. 149, 153.
1915. *Palasterina bonneyi*, Schuchert, *loc. cit.*, pp. 15 , 152, 153.
1916. „ *primæva*, Spencer, this Monograph, pl. iv, fig. 6.

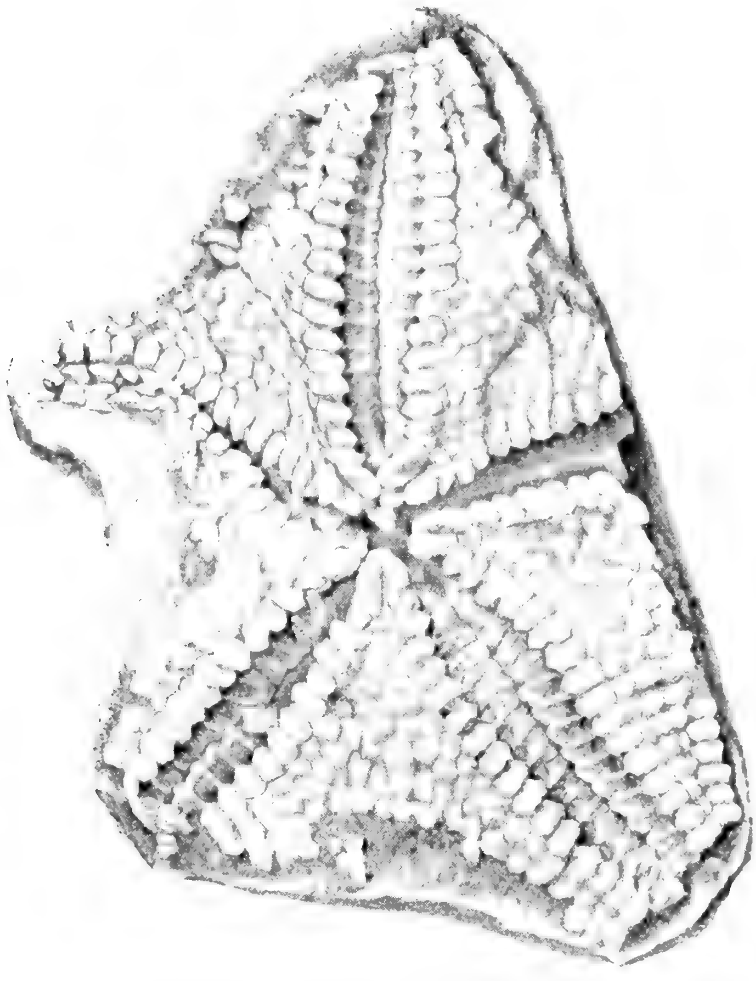
Material.—I have placed in this species five specimens showing the oral surface, two being from the same horizon:

(1) The type of *Lindströmaster antiquus*, in the Angelin Collection of the Mineralogical Museum, Copenhagen (no. 306), from the Ludlow of Gotland.

(2) A new specimen from the Wenlock of Dudley, in Sir Charles Holcroft's collection at the museum of the University of Birmingham (no. 1).

(3) A new specimen from the Wenlock of Gutterford Burn, in the Royal Scottish Museum, Edinburgh.

The fourth and fifth specimens are from a slightly higher horizon, the Lower Ludlow of Church Hill quarries, Leintwardine, and are in the British Museum (Nat. Hist.). One of these is the type of Gregory's species *P.* "*bonneyi*," and shows both oral and apical surfaces (no. 40299). The second specimen shows only the apical surface (no. 40301).



TEXT-FIG. 165.—Liljevall's original drawing of *Palasterina antiqua* (reproduced from 'Geol. Mag.,' 1899, pl. xvi, fig. 1 *b*). × 4.

Although there are differences between the specimens I think that they can be best explained as due either to the age of the individual animal, accidents in preservation, or slight differences in the geological horizon.

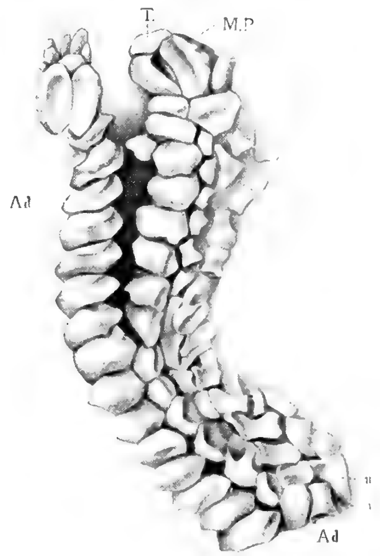
Specific Characters.—See p. 220.

(1) *Description of Type-Specimen from Gotland* (*Text-fig.* 165).

If we turn to the illustration (Text-fig. 165), we observe that at first sight there are, apparently, infero-marginalia at both sides of the arms pointing S.E. and

N., that is, we seemingly have a pentagonal form with large ventral interradial areas bounded by infero-marginalia, many of which have fallen away. It was this appearance which led Gregory to place the form among the Phanerozonate Asteroidea. Gregory stated that "both supero- and infero-marginals are present." I cannot see any trace of supero-marginals.

Schuchert (1915, p 149), in his remarks on this species, stated that "it is probable that the marginals in *Lindströmaster* which Gregory thinks are both supra- and infra-marginals lying directly superposed are only infra-marginals." He also states that "when more material is obtained and the genus is re-studied, comparisons should also be made with *Palasterina primæra*, as the two forms



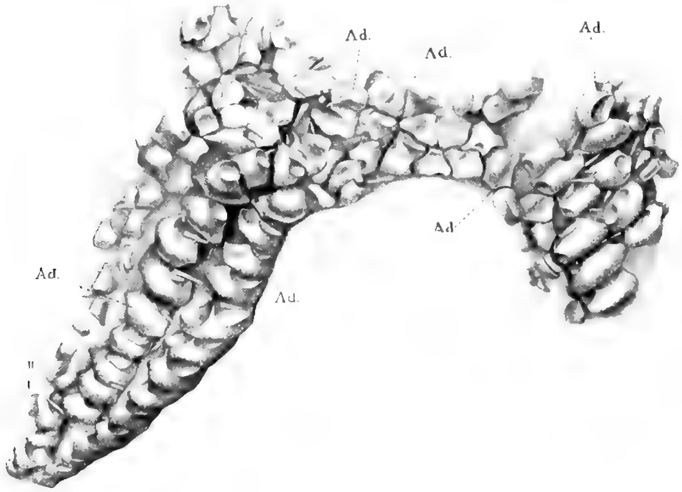
TEXT-FIG. 166.—Drawing of an arm of *Palasterina antiqua* (type-specimen). *Ad.*, adambulacral; *M.P.*, mouth-angle plate; *T.*, torus. × 5.

appear to have much in common." Prof. Lindström, who lent the specimen to Gregory, referred the form to *Palasterina*.

If the form belonged to *Palasterina*, many of the ossicles in the interradii must be really ossicles from the lateral surfaces squeezed into their present position by post-mortem distortion. Both the original drawing and an electrotype of the specimen in the collection of the British Museum (Nat. Hist.) suggested that this was the case, and in order to clear the matter up I applied to the authorities of the Copenhagen Museum for permission to re-examine the specimen. By the courtesy of Dr. Ravn this was granted.

The arm pointing east was cleared of matrix and turns out to be a long cylinder stretching to within a short distance of the odontophor. The plates in the interradius are therefore those squeezed over from the neighbouring arm. A drawing has been made of the first-mentioned arm (Text-fig. 166), and it illustrates well the cylindrical structure and the typical *Palasterina* appearance. The mouth-angle plates are almost exactly similar to those of *P. primæra*, and the adambulacralia are stout with a coarse, pustulose ornament. Alongside the adambulacralia are the small accessory plates seen in the type species. These are succeeded by almost oblong infero-marginalia. At the extremity of the arm are a few swollen apical plates similar to those figured in Text-fig. 158, p. 221.

The mouth-angle plates carry a torus with stout flat spines. The oral surfaces of the adambulacralia are not so rounded as in *P. primæva* but almost identical with the same surfaces in *P. follmanni*. The groove in this arm is closed over but is open in other arms (Text-fig. 165). The ambulacralia are closely similar to those in *P. primæva*, except that they have a slight thickening where they overlap the preceding plate. An odontophor is visible in the interradial angle. The arms are distinctly petaloid.



TEXT-FIG. 167.—Drawing of an arm and the base of a second arm of *Palasterina antiqua* (from specimen in University of Birmingham Museum). *Ad.* indicates rows of adambulacralia. × 5.

Measurements.—None of the arms is visible in full length, although it is probable that the arm pointing east is nearly so. This possesses seventeen adambulacralia and has R = 16·5 mm., r = approximately 6 mm.

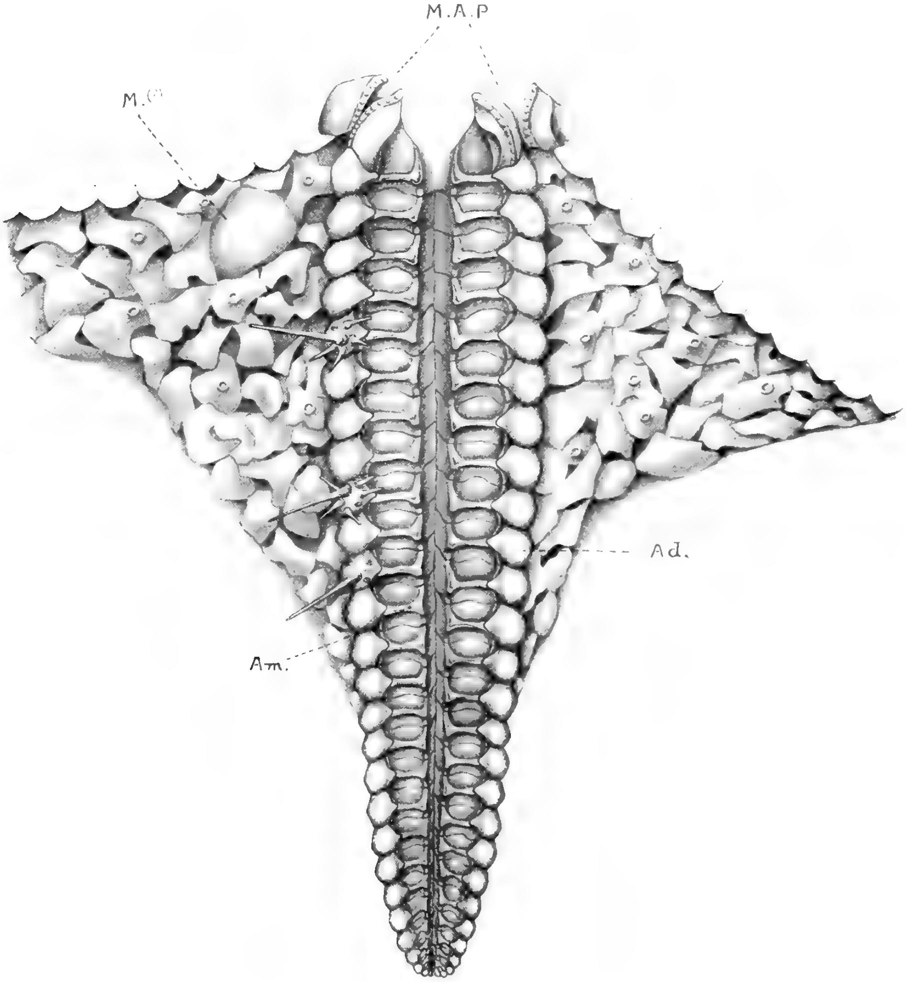
Horizon and Locality.—Originally given as Lower Wenlockian (Bed C), but the Hamra Limestone is now correlated with Upper Ludlow; S. Udde, Gotland.

(2) *Description of the Specimen from the Wenlock Limestone of Dudley (Text-fig. 167).*

The mouth-region of the specimen seems to be imperfect and mouth-angle plates are not recognisable. In spite of this, there can be no hesitation in referring the specimen to *Palasterina*. The general form of the arm and the stout, swollen adambulacralia are exactly similar to those of *P. primæva*, except that they do not seem to show a ridge. The first few adambulacralia are rather irregular in form and remind one of the proximal adambulacralia in *Lepidactis wenlocki* (see p. 115). The stout adambulacral spines are preserved. Alongside the adambulacralia is the usual row of accessory plates. Beyond these again is a row of swollen infero-marginalia. The plates filling up the interradial areas are rather irregular in shape.

Measurements.—The specimen is of almost exactly the same size as the type of the species. R. is approximately 17 mm. and there were apparently about 18 adambulacralia on each side of an arm; r. is approximately 6 mm.

Horizon and Locality.—Wenlock Limestone; Dudley, Worcestershire.



TEXT-FIG. 168.—Drawing of an arm and the neighbouring interradii of *Palasterina antiqua* (specimen previously referred to *Palasterina bonneyi*, Gregory). *Ad.*, Adambulacralia; *Am.*, ambulacralia; *M.* (?), madreporite?; *M.A.P.*, mouth-angle plate. × 10.

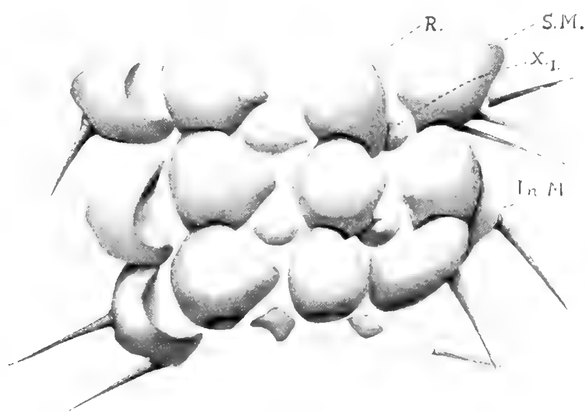
Remarks.—The specimen differs from the type in the swollen nature of the adambulacralia and the greater irregularity of the interradial plates. These do not seem to me to warrant specific distinction. In the absence of more material I do not think it is advisable to name the variety.

(3) *Description of* "Palæasterina bonneyi" (*Pl. XVI, fig.* 2; *Text-fig.* 168).

Material.—Two imprints, one with counterpart, in the British Museum (Nat. Hist.), nos. 40299 and 40301 respectively. The former is the specimen described by Salter as *P. primævus* in 1857. Gregory later described it as a new species, *P. bonneyi*, but neither he nor other authors appear to have recognised that the specimen was the "*P. primævus*" of Salter. The form has been somewhat distorted by post-mortem pressure. Specimen 40301 shows the apical surface only.

Oral Surface (Pl. XVI, fig. 2; Text-fig. 168).—The groove has been forced widely open and in consequence appears to be shallow. The ambulacralia are exposed in full length. They are opposite or slightly alternating in the proximal region, distinctly alternating distally, and have the usual structure associated with these primitive forms. The small size of the adambulacralia makes their ornament difficult to determine. So far as one can see, there was no distinct adambulacral ridge, but the spines seem to have been distributed all over the face of the ossicle. The majority of the spines appear to have been long.

The mouth-angle plates look like poorly preserved smaller editions of the corresponding structures in *P. primæva*.



TEXT-FIG. 169.—Drawing of a small portion of the apical surface of an arm of *Palasterina antiqua* (= *P. bonneyi*). *In.M.*, inter-marginalia; *R.*, radial; *S.M.*, supero-marginal; $x_{\cdot 1}$, adradial. × 20.

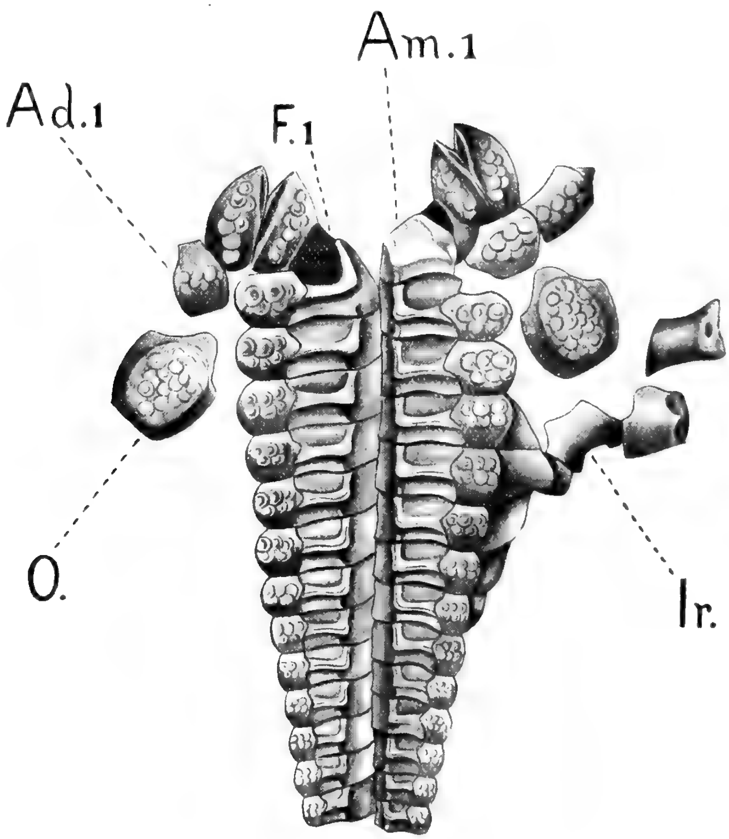
The interradial areas are much more extensive than in *P. primæva*, but the extent varies so much in the different radii (Pl. XVI, fig. 2) that one can only suppose that the body was considerably swollen during life, and that the plates now seen on the oral surface once formed the lateral interradial walls of the disc. The plates are not pavement-like, as in Gregory's figures, but rounded. Some show rounded articulations for spines. A plate shaded in the figure may represent the madreporite, but one cannot be certain of the madreporiform markings.

Apical Surface (Pl. XVI, fig. 1; Text-fig. 169).—The apical surface is so very like that of *P. primæva* that I do not consider it necessary to figure it in detail. One must note, however, that certain of the plates in the centre of the disc which are visible in the photograph, and have been previously figured as disc plates, are really the mouth-angle plates pushed through the apical covering after death. Adradialia are more numerous than is usual in *P. primæva*, but this one would expect because of the swollen nature of the arms.

Measurements.—R is 13·5 mm.; r varies from 5 mm. to 6·5 mm.

Horizon and Locality.—Upper Silurian (Lower Ludlow); Church Hill Quarry, Leintwardine, Salop.

Remarks.—The presence in the fossils of large areas in some of the interradii gives a very strong resemblance to the type. The interradial plates are more irregular than in the type. The adambulacral spines appear to be longer than is usual in other specimens of *Palasterina*.



TEXT-FIG. 170.—Oral view of a portion of the disc and arm of *Palasterina antiqua* (specimen in Royal Scottish Mus.). *Ad.*$_1$, first adambulacral; *Am.*$_1$, first ambulacral; *F.*$_1$, the cup for the first tube-foot; *Ir.*, interradial plates; *O.*, odontophor. × 25.

(4) *Description of the Small Form from Gutterford Burn* (Pl. XV, fig. 9; Text-fig. 170).

Material.—One mould in sandstone in the Royal Scottish Museum, Edinburgh. The oral surface only is shown, and that rather imperfectly.

Description.—Text-fig. 170 gives a portion of one arm and the neighbouring interradii. The mouth-angle plates are of the usual *Palasterina* type, swollen, with a wide gape and showing the inner coarsely ornamented area. The groove is widely open and has obviously suffered somewhat from post-mortem distortion. The ambulacralia are as in "*P. bonneyi.*" The adambulacralia also are much as in that form. The ornament is very conspicuous and there is no ridge.

The first adambulacral is the largest. The arm must have been uniformly tapering, not petaloid.

The interradii may extend to about the fourth or fifth adambulacral. There is considerable variation in the different interradii. Some show no ossicles except the odontophor. This latter plate has considerable resemblance in general form to that in *Eoactis*, and suggests that *Palasterina* descended from a form with a conspicuous odontophor. It differs from the odontophor in *Eoactis* in being more swollen and in possessing a coarse pustulose ornament.

Measurements.—R : r :: 4 mm. (approx.) : 2 mm.

Horizon and Locality.—Wenlockian (Starfish Bed); Gutterford Burn, Pentland Hills.

3. **Palasterina follmanni,** Stürtz. Plate XVI, figs. 3—7; Text-fig. 171.

1890. *Palasterina follmanni*, Stürtz, Palæontographica, vol. xxxvi, p. 226, pl. xxix, figs. 29—31 *a*.
1900. *Pseudopalasterina follmanni*, Stürtz, Verhandl. naturhist. Ver. preuss. Rheinl., vol. lvi, pp. 219, 224.
1914. *Pseudopalasterina follmanni*, Schuchert, Fossilium Catalogus, Animalia, pt. 3, p. 36.
1915. *Pseudopalasterina follmanni*, Schuchert, Bull. 88, U.S. Nat. Mus., pp. 156, 157.

Material.—There are nine specimens of this species in the British Museum (Nat. Hist.), three figured by Stürtz (nos. E. 3469, fig. 29; E. 3470, figs. 30, 30 *a*; E. 3471, fig. 31), the remaining six registered as E. 5004 (specimen mentioned by Stürtz, p. 224), E. 13625, E. 13626, E. 13629, E. 13635 and E. 13636.

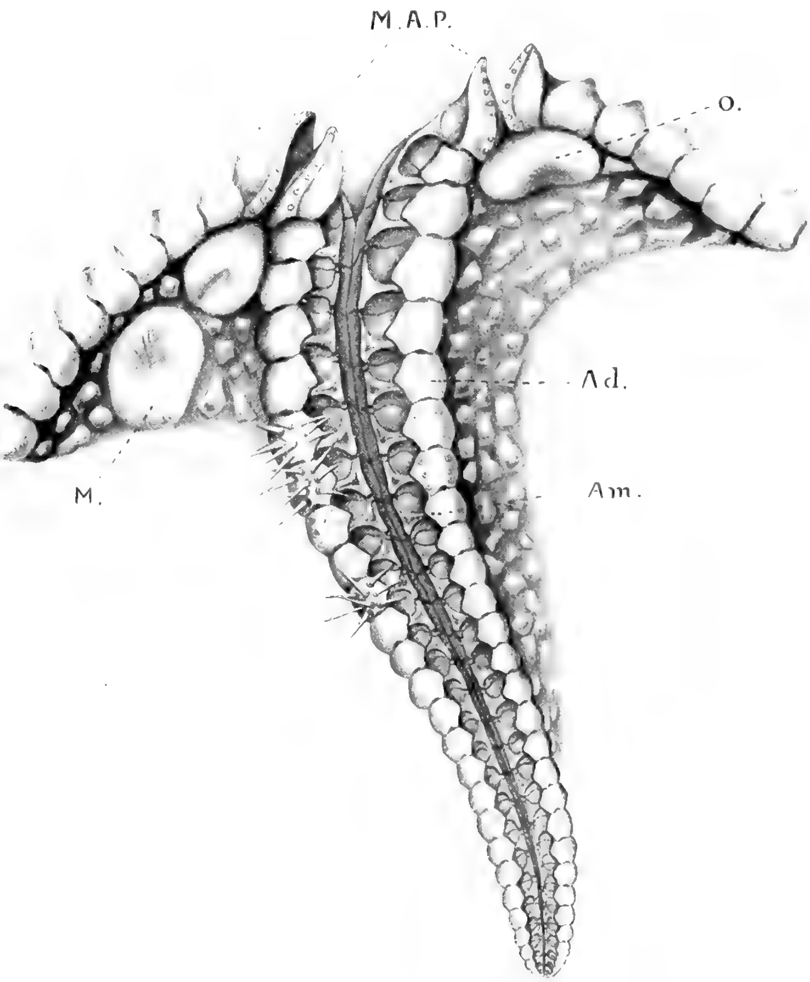
The photographs given on Pl. XVI are designed to show the somewhat varying appearances due to differences in fulness of growth. The smaller specimens are compact in appearance, and post-mortem compression has not greatly changed their outline. Age in the individual seems to have been accompanied by a considerable increase in the height of the arm. The general surface of the body becomes, in consequence, more slightly built, and post-mortem compression causes considerable distortion. The specimen photographed in Pl. XVI, fig. 4, has had its arms distorted by lateral compression, but the ossicles remain for the greater part in their original apical position. That photographed in fig. 7 has been subject to dorso-ventral compression, and the apical ossicles are forced into some of the oral interradial areas. The series is valuable in supporting the view that in other species of *Palasterina*, in which the material is not nearly so complete, the large interradial areas are produced secondarily and were not a feature of the living form.

In several of the specimens the distal half of one or more arms is bent back, so that, if only the oral surface be seen, the arms appear to be much foreshortened.

This is noticeably the case in E. 13629 (Pl. XVI, fig. 6), where all the arms have been preserved in this way.

Specific Characters.—See p. 220.

Oral Surface (Pl. XVI, figs. 3—7; Text-fig. 171).—The text-figure is drawn from one of the smaller individuals (R = 36 mm.). The mouth-angle plates are of the typical *Palasterina* type. Immediately behind them is a stout odontophor as in *P. scotiæ*, but it is not swollen or ornamented as in that form. Behind the odontophor in the left interradius is a large madreporite of the same form as that



TEXT-FIG. 171.—Drawing of an arm and the neighbouring interradii of *Palasterina follmanni*. *Ad.*, adambulacralia; *Am.*, ambulacralia; *M.*, madreporite; *M.A.P.*, mouth-angle plates; *O.*, odontophor. ×2.

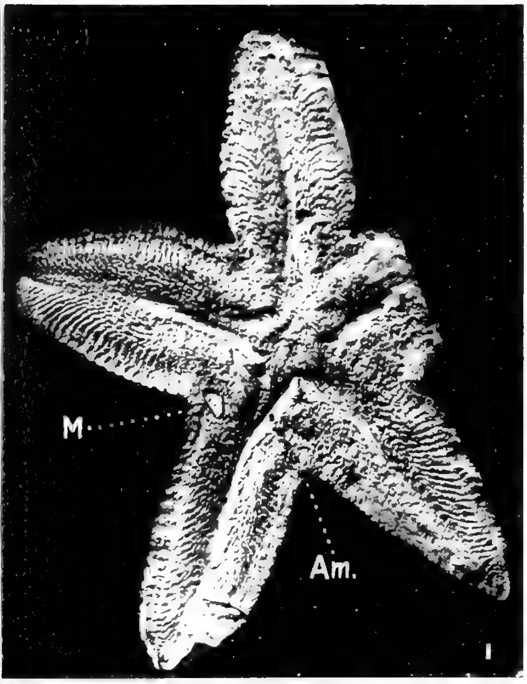
in *P. primæva*. The remaining plates in the interradii are small and identical in shape and ornament with those on the apical surface.

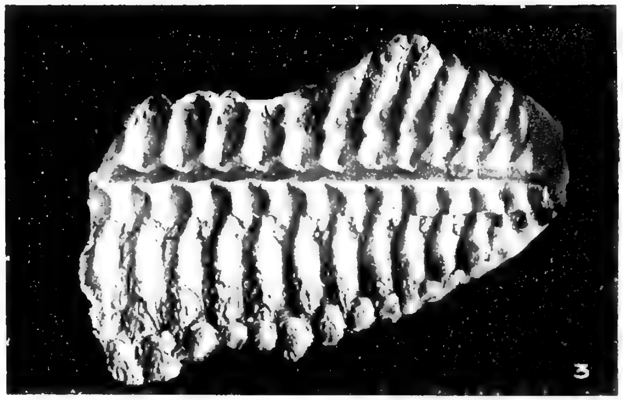
The groove is widely open and the ambulacralia are seen clearly. They are of the primitive type found in the forms of this lineage. They seem to be opposite throughout the length of the arm drawn. This is the condition in three of the arms of the specimen. In the other two arms the ambulacralia alternate in the distal region. The adambulacralia are only slightly swollen on their ornamented surface. The ornament consists of three groove-spines and stout sub-ambulacral spines distributed uniformly over the plate.

PLATE XIV.

Fig.		Page.
1.	*Platanaster ordovicus*, n. sp.; photograph of the apical surface, nat. size.—Upper Ordovician (Caradocian); Cound, Madeley, Salop. Museum of Practical Geology, Jermyn St., no. 8238.	171.
2.	Ditto; photograph of the oral surface of the counterpart of the same specimen, nat. size. Museum of Practical Geology, Jermyn St., no. 25347.	171.
3.	Ditto; photograph of a portion of oral surface of the arm of the same specimen, × 4.	171.
4.	*Palasteriscus devonicus* (Stürtz); photograph of the apical surface, two-thirds nat. size.—Lower Devonian; Bundenbach, Germany. British Museum (Nat. Hist.), no. E. 5026.	176.
5.	*Schuchertia wenlocki*, n. sp.; photograph of the oral surface, × 2.—Middle Silurian (Wenlock); Gutterford Burn, Pentland Hills. Royal Scottish Museum, no. 32/485.	215.
6.	Ditto; photograph of a portion of the oral surface of another individual, × 2.—Ibid. Royal Scottish Museum, no. 32/484.	215.

M. = madreporite; M.P. = mouth-angle plate.


M
Am.
1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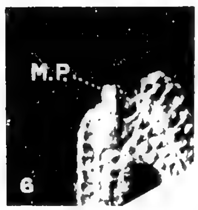
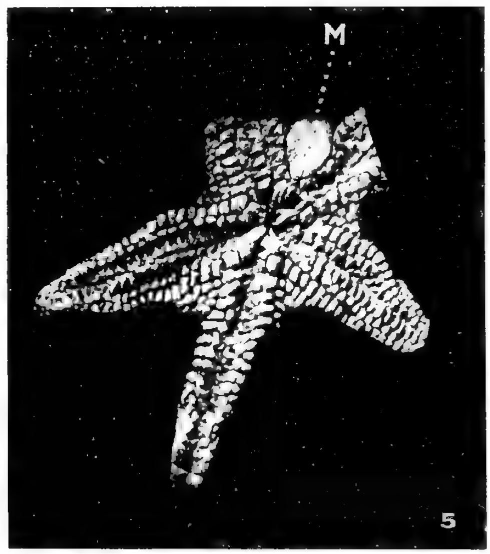
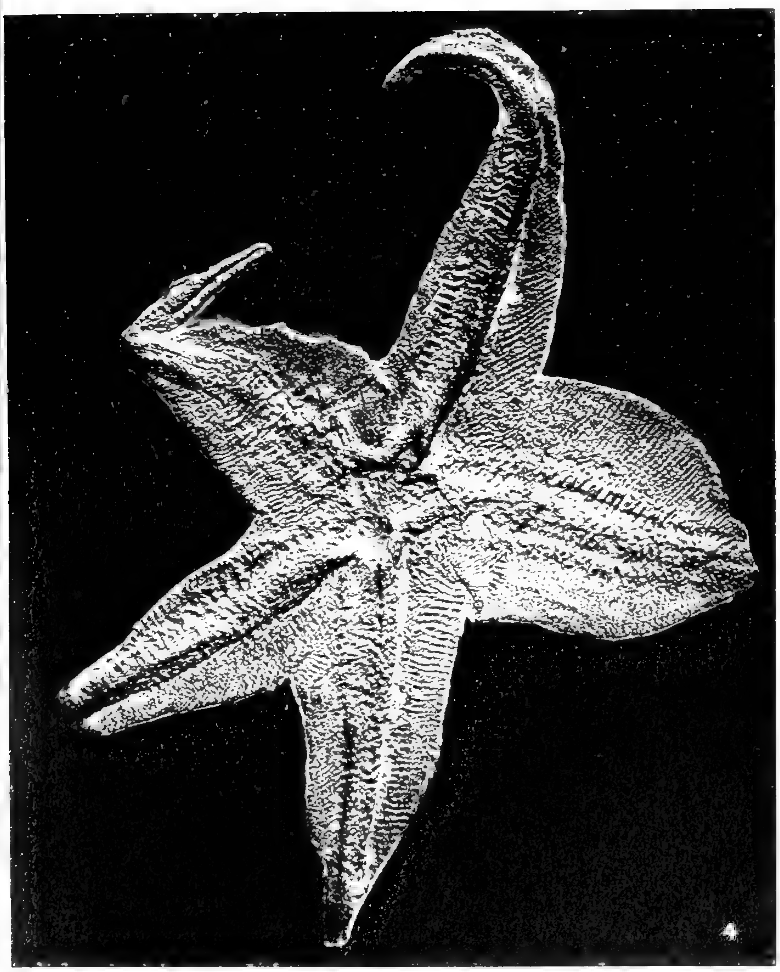

M.P.
6


M
5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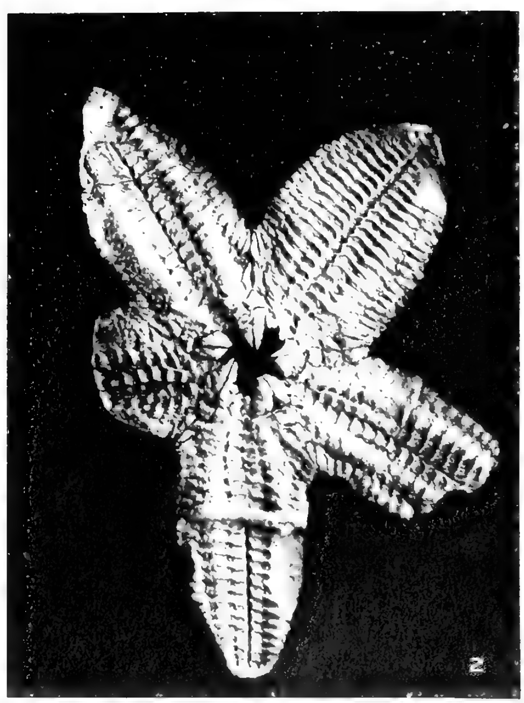
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PLATE XV.

Fig.		Page.
1.	*Schuchertia laxata*, Schuchert; photograph of the apical surface, × 2.—Upper Ordovician (Ashgillian); Thraive Glen, Ayrshire. Mrs. Gray's Collection, no. D. 330.	212.
2.	*Schuchertia wenlocki*, n. sp.; photograph of a portion of the oral surface to show detailed structure of the ambulacral groove, × 10.—Middle Silurian (Wenlock); Gutterford Burn, Pentland Hills. Royal Scottish Museum, no. 32/484.	215.
3.	Ditto; photograph of an interradial angle of the specimen figured Pl. XIV, fig. 5, × 3.	215.
4.	Ditto; photograph of a portion of the apical surface, × 2.—Ibid. Royal Scottish Museum, no. 32/480.	215.
5.	*Palasterina primæva* (Forbes); photograph of the apical surface of one of Forbes' types, × 3.—Upper Silurian (Lower Ludlow, Bannisdale Slates); High Thorns, Underbarrow, Westmoreland. Sedgwick Museum, Cambridge, no. a/517 (slab d).	223.
6.	Ditto; photograph of the apical surface of another individual, × 4½.—Bannisdale Slates; ? Underbarrow. Sedgwick Museum, Cambridge, no. 48.	223.
7.	Ditto; photograph of the oral surface of another individual, × 4½.—Ibid. British Museum (Nat. Hist.), no. E. 4991.	223.
8.	*Eoactis simplex*, Spencer; photograph of the oral surface, × 4½.—Lower Ludlow or Upper Wenlock; Hafod, Llandovery. British Museum (Nat. Hist.), no. E. 13154.	206.
9.	*Palasterina antiqua* (Hisinger); photograph of the oral surface of young individual, × 4½.—Middle Silurian (Wenlock); Gutterford Burn, Pentland Hills. Royal Scottish Museum, no. 32/463.	228.

M. = madreporite; M.P. = mouth-angle plate; O. = odontophor.

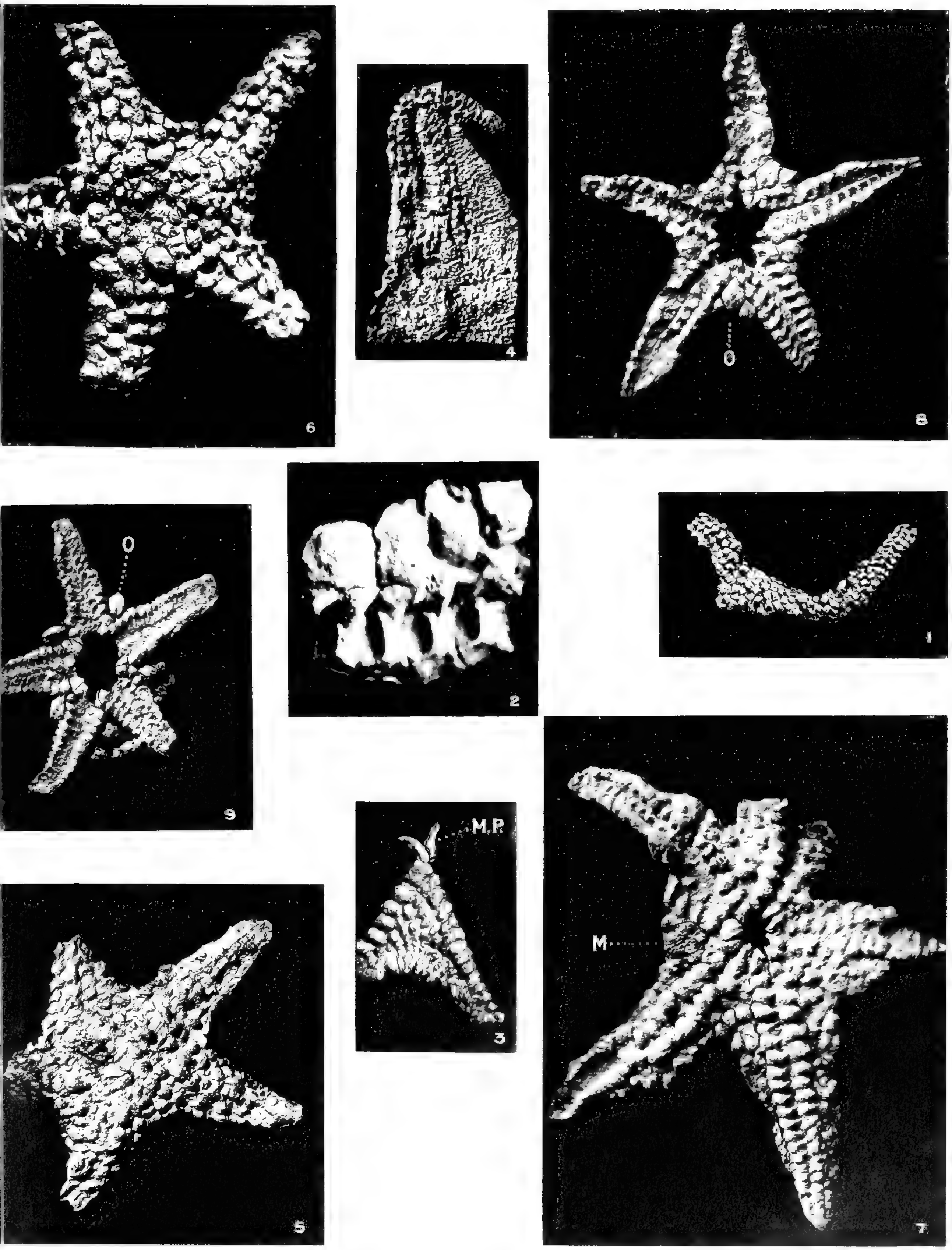

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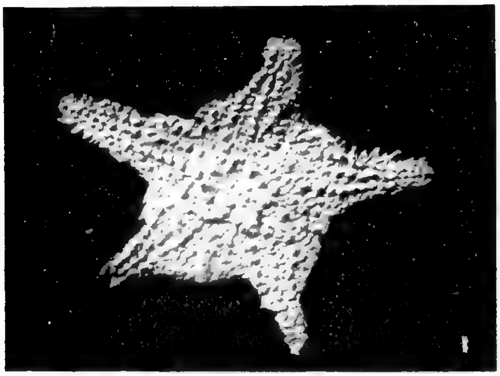
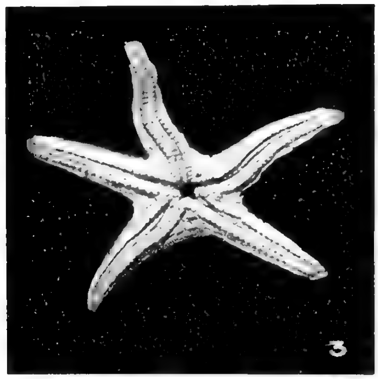
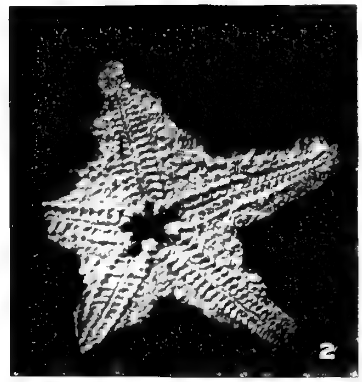
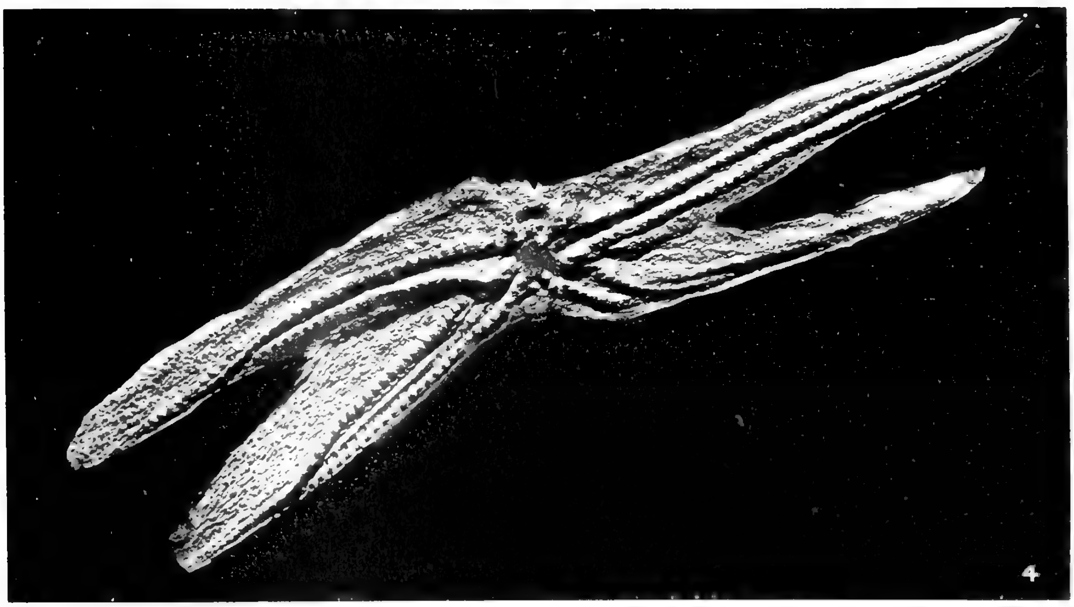
PLATE XVI.

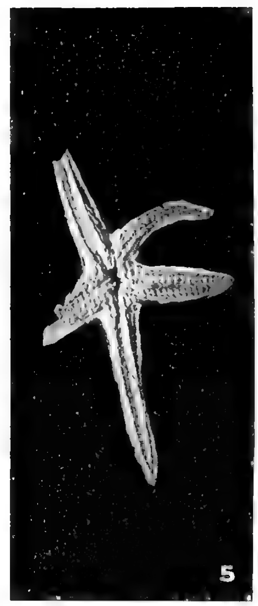
Fig.		Page.
1.	*Palasterina antiqua* (Hisinger); photograph of the apical surface, × 2. —Upper Silurian (Lower Ludlow); Leintwardine, Herefordshire. British Museum (Nat. Hist.), no. 40299.	228.
2.	Ditto; photograph of the oral surface, the counterpart of the specimen photographed in fig. 1, × 2.	228.
3.	*Palasterina follmanni*, Stürtz; photograph of the oral surface, × $\frac{3}{5}$.—Lower Devonian; Bundenbach, Germany. British Museum (Nat. Hist.), no. E. 13635.	235.
4.	Ditto; photograph of the oral surface, × $\frac{3}{5}$.—Ibid. British Museum (Nat. Hist.), no. E. 13625.	235.
5.	Ditto; photograph of the oral surface, × $\frac{3}{5}$.—Ibid. British Museum (Nat. Hist.), no. E. 13636.	235.
6.	Ditto; photograph of the oral surface, × $\frac{3}{5}$.—Ibid. British Museum (Nat. Hist.), no. E. 13629.	235.
7.	Ditto; photograph of the oral surface, × $\frac{3}{5}$.—Ibid. British Museum (Nat. Hist.), no. E. 13626.	235.
8.	*Schuchertia stellata* (Billings); photograph of the oral surface, × 4.—Middle Ordovician (Trenton); Ottawa, Canada. Geological Survey of Canada, no. 1399. (Reproduced from Schuchert, *op. cit.*, pl. xxxii, fig. 2.)	211.

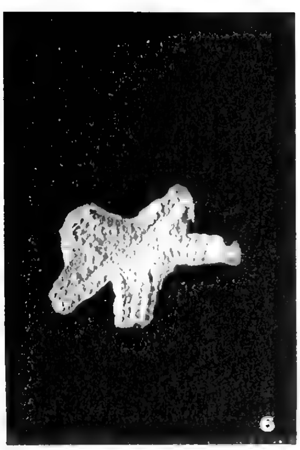












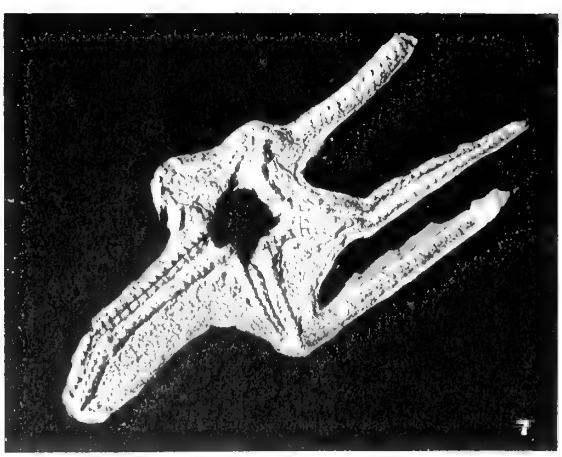


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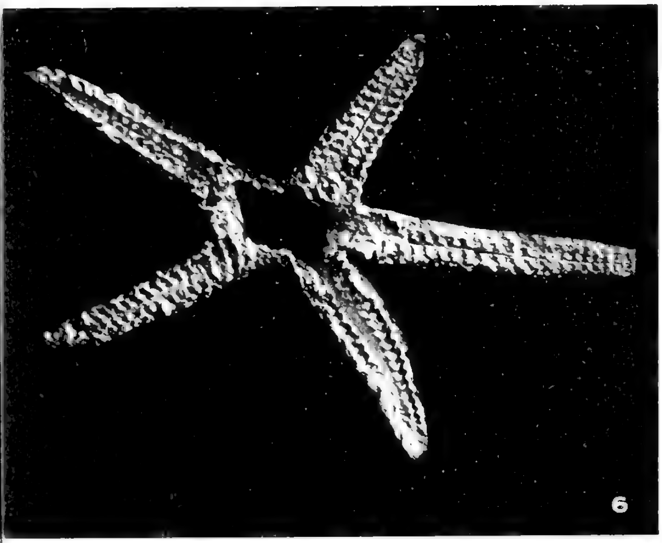
PLATE XVII.

FIG. PAGE.

1. *Baliactis ordovicus*, n. gen., n. sp.; photograph of the oral surface, × 2.—Upper Ordovician (Caradocian); Habberley Brook, Shropshire. Shrewsbury Museum.
2. *Baliactis wenlockensis*, n. sp.; photograph of the oral surface, × 3½.—Middle Silurian (Wenlock); Gutterford Burn, Pentland Hills. Royal Scottish Museum, no. 32/439, 1897.
3. *Palasterina primæva* (Forbes); photograph of the oral surface of a group of individuals on the same slab, nat. size.—Upper Silurian (Ludlow); Westmoreland. Kendal Museum. 223.
4. *Tæniactis wenlocki*, n. sp.; photograph of individual with arms flexed upwards over the disc, × 4.—Middle Silurian (Wenlock); Gutterford Burn, Pentland Hills. Royal Scottish Museum, no. 32/522, 1897.
5. Ditto; photograph of the oral surface, × 4.—Ibid. Royal Scottish Museum, no. 32/498, 1897.
6. *Palæura ?*; photograph of the oral surface, × 1–2.—Ibid. Royal Scottish Museum, no. 32/469, 1897.



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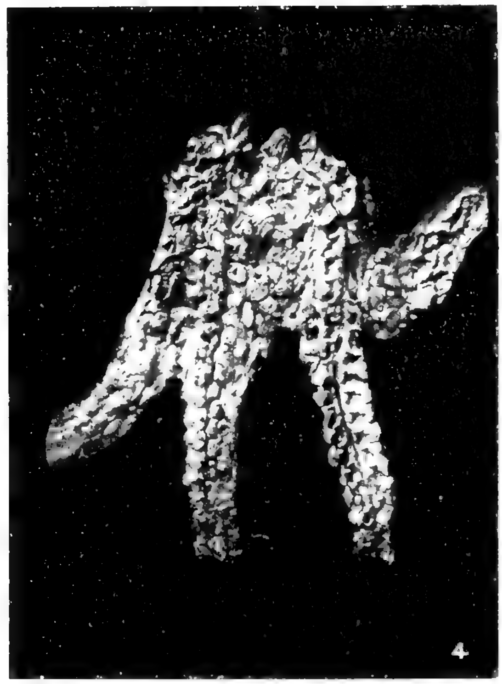

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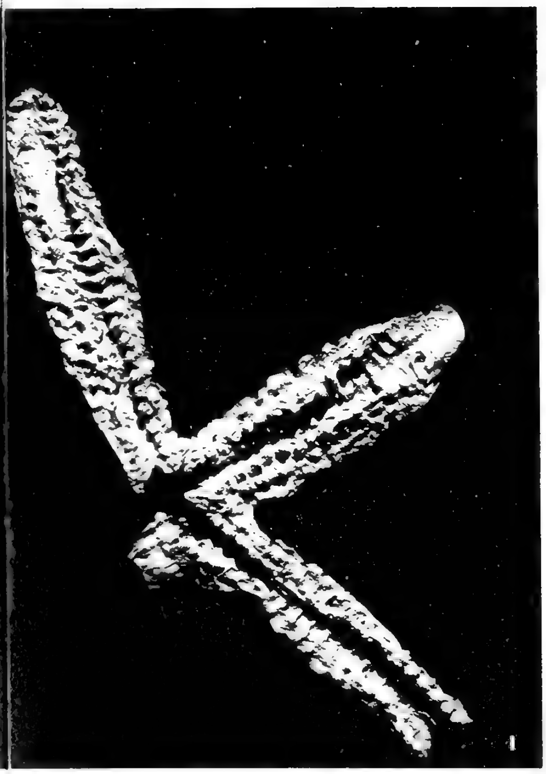

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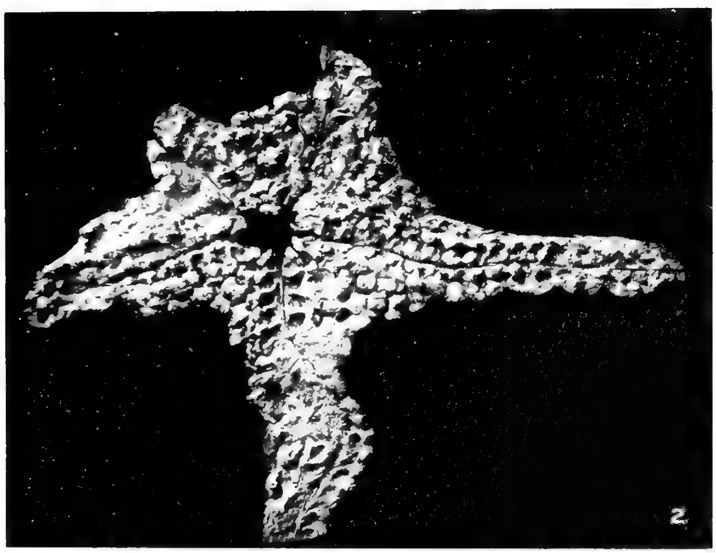

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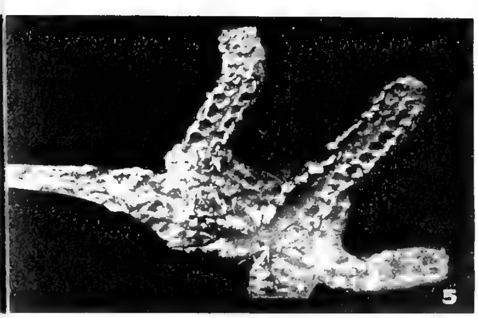

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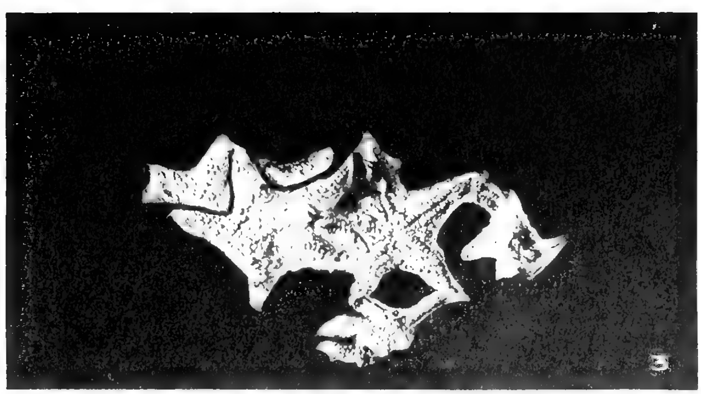

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Palæontographical Society, 1920.

A MONOGRAPH

OF THE

FOSSIL INSECTS

OF THE

BRITISH COAL MEASURES.

BY

HERBERT BOLTON, M.Sc., F.R.S.E., F.G.S.,
DIRECTOR OF THE BRISTOL MUSEUM.

PART II.

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LIST OF TEXT-FIGURES.

PREFACE.

This monograph owes its existence to the friendly encouragement of Dr. A. Smith Woodward, F.R.S., Keeper, and of Dr. F. A. Bather, F.R.S., Deputy-Keeper of the Geological Department of the British Museum (Natural History), and to these gentlemen I am indebted for the loan of the undescribed Coal Measure fossil insects in their charge, and for much helpful assistance in other ways.

Others to whom my thanks are due are the Director of the National Museum, Washington, U.S.A.; Dr. F. L. Kitchin, of the Museum of the Geological Survey; Mr. G. W. Lee, of the Scottish Geological Survey; Dr. J. A. Clubb, of the Derby and Mayer Museums, Liverpool; Dr. W. E. Hoyle, of the National Museum of Wales, Cardiff; Prof. W. S. Boulton, of the Birmingham University; Dr. W. M. Tattersall, of the Manchester Museum, Victoria University; Mr. L. Gill, M.Sc., of the Hancock Museum, Newcastle; Mr. H. Y. Simpson, of the Kilmarnock Museum; and Messrs. Eltringham, S. Priest, W. Egginton, and D. Davies.

To Mr. W. J. Tutcher I am deeply indebted for his ready assistance in photographing all the various specimens submitted for examination. His remarkable skill has been always at my service, and by means of it I have been able to determine many details of structure which otherwise would have remained obscure.

I am indebted to the Royal Society for several grants towards the cost of the work.

H. BOLTON.

Family Coseliidæ, nova.

A group of large-winged insects in which the principal veins are openly spaced; the radial sector joined by an outer branch of the median, and the median sending a strong inward commissure to the cubitus.

The family shows relationships with the Œdischiidæ, Omaliidæ, and Cacurgidæ.

Genus **COSELIA**, novum.

Generic Characters.—Costa and subcosta feeble, intercostal area very wide; radius straight; radial sector arising near middle of wing. Cubitus **S**-shaped, its branches occupying most of the inner margin of the wing. Interstitial neuration of transverse nervures uniting in some areas to form an open meshwork.

Coselia palmiformis, sp. nov. Plate V, fig. 3; Text-figure 25.

Type.—Basal half of a left wing in counterpart in an ironstone nodule; British Museum (Johnson Collection, no. I. 15893).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

Specific Characters.—Subcosta united to radius basally, giving off numerous branches, united by irregular cross-nervures, to the outer margin. Radius strong, divergent from subcosta. Radial sector diverging from the radius. Median steadily divergent from radius and radial sector, and giving off an inner branch in the first third of the wing to the main stem of the cubitus. Beyond the middle of the wing, the median sending off several outer branches, the first uniting with the radial sector. Cubitus with its divisions extending over the greater portion of the inner margin of the wing. First anal vein strongly curved, the next thrice forked.

Description.—This species is represented by a little over the basal half of a left wing, 54 mm. long and 26 mm. wide, showing the under surface only. The outer or costal margin is convex and very thin. The costal area very wide at its base (6 mm.) and diminishing towards the wing-apex.

The subcosta is a feeble vein, apparently united basally to the radius, and passing outwards in a straight line towards the distal end of the outer margin, or into the outer part of the wing-apex. It gives off numerous branches to the outer margin, the branches being disposed regularly, and inclining apically in their course. They are joined by a few irregular cross-nervures, most of which are at right-angles to the branches of the subcosta.

The radius arises with an inward curve near the point at which the subcosta is given off, diverging from it and following a straight line to the wing-apex.

The radial sector arises near the middle of the wing, and at a distance of 38 mm. from the wing-base. The angle which it makes with the radius is fairly large, and the enclosed area must have been very wide in the outer half of the wing.

The median arises close to the radius, and then bends inwards as it passes to the inner half of the wing-apex. Its divergence from the radius is more than double that of the radius from the subcosta. Portions of two outwardly directed branches are shown, the first joining the radial sector; only the base of the second is preserved; it follows a course parallel with the first branch. About 21 mm. from the base the median gives off a strong inward branch passing obliquely to the cubitus and fusing with it. The cubitus is **S**-shaped, being convex outwardly to the junction with the commissural vein from the median, and concave inwardly afterwards. Owing to this inward inflexion, that part

FIG. 25.—*Coselia palmiformis*, gen. et sp. nov.; diagram of basal portion of left wing, showing the general character of the venation, three-halves natural size.—Middle Coal Measures: Coseley, Staffordshire. Johnson Collection, Brit. Mus. (no. I. 15893).

of the cubital area lying beyond the junction with the median is extremely wide. The cubitus gives off four inwardly directed branches at wide intervals, the first branch having a wide forking in the first third of its length. The branches of the median must have occupied the greater part of the inner margin of the wing.

The cubitus gives off six inward branches, the first arising very low down, and the remaining five at regular intervals, the first being given off a little way beyond the junction with the commissural vein. The first and fourth of these branches fork into two widely separated twigs.

The first anal vein is simple, and has a broad convex outward sweep down to the inner margin; the second anal vein gives off three branches on its inner side. Other anal veins may have been present, but the wing-structure is missing at this point.

With the exception of the subcosta and radius, all the main veins are widely spaced, and no branches are given off, except the first median, in the basal third of the wing.

The interstitial neuration is well marked, and of unusual character. That of the intercostal area has been already described; that between the subcosta and radius, between the radius and radial sector, and between the radial sector and the median, consists of a few irregular cross-nervures, one or two of which unite. In the median-cubital area the cross-nervures are joined up by longitudinal branches following a zig-zag course. A similar neuration is seen between the inner branches of the cubitus, while the anal area is crossed by irregular cross-nervures occasionally uniting, as in the fore-part of the wing.

Affinities.—The general characters agree most closely with those of the Cacurgidæ, a family of insects which Handlirsch has described from ironstone nodules found in and around Mazon Creek, Illinois, U.S.A. It comprises insects which possess well-marked characters, but which, as a whole, Handlirsch is unable to assign with certainty to the Protorthoptera, or to the Protoblattoidea (Handlirsch, 'Amer. Journ. Sci.' [4], vol. xxxi, 1911, p. 323).

The wing of *Cacurgus spilopterus*, Handlirsch, has the same wide costal area; the radial sector arises far out, and the median gives off a commissural vein to the cubitus. The central portions of the median and cubital areas are also very wide, and the anal veins have the same strong inward curve.

The interstitial neuration is much similar, but the formation of a meshwork has not proceeded so far in the British specimen as in *Cacurgus spilopterus*, where it is present between all the main veins, except the costal and subcostal. In the British specimen the meshwork is chiefly developed in the median and cubital areas. Areolæ are present in the wings of both species.

The differences between the wings of the two species are, however, important. In *Cacurgus spilopterus*, the first branch of the median does not unite with the radial sector, nor does it approach it very closely, whereas in the British wing, the first outer branch must have united with the radial sector. The median also branches again further out, the median in *C. spilopterus* having one outer branch only. *Lithosialis brongniarti* (Mantell) shows less affinity to the wing, but possesses the wide costal area, the same irregular and ramified interstitial neuration, but a more complex median and simpler cubitus. The commissural vein is also wanting.

One other form with which a comparison needs to be made is *Omalia macroptera*, Van Beneden and Coemans. This species was obtained from the Westphalian (Middle Upper Coal Measures) of Hainault, Belgium. In its wing the costal area is wide, and crossed by oblique branches from the subcosta; the median sends an outer branch to join the radial sector, but there is no union of the median and cubitus. The interstitial neuration is not mesh-like.

These wings are so similar that there seems no doubt they are closely related, but the relationship of the British specimen is closest with the genus *Cacurgus*.

Family Œdischiidæ, Handlirsch.

1906. Handlirsch, Proc. U.S. National Museum, vol. xxix, p. 700, and Die Fossilen Insekten, p. 142.
1919. Handlirsch, Revision der Paläozoischen Insekten, p. 39.

Radial sector coalescing with the main stem of the median, and branching as if a part of the latter vein.

Handlirsch regards the family as closely related to the Sthenaropodidæ.

Genus **GENENTOMUM**, Scudder.

1885. *Genentomum*, Scudder, Mem. Bost. Soc. Nat. Hist., vol. iii, p. 329.
1893. *Œdischia*, Brongniart, Faune Entom. Terr. Prim., p. 559.

Generic Characters.—Wings about three times as long as wide; principal veins and their branches well spaced, and united by a series of straight and well-defined nervures. Apex of wing obtuse.

Considerable doubt exists as to the true relationship of this genus, Scudder referring it to the Homothetidæ, Brauer considering it to have affinity with the Sialidæ, while Brongniart placed it with the Œdischiidæ.

Genentomum (?) subacutum, Bolton. Plate V, fig. 4.

1911. *Genentomum subacutum*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 334, pl. xxvii, figs. 18, 19.

Type.—Two small wing-fragments, 9 mm. in length, and 6 mm. in breadth; Bristol Museum (no. C. 972).

Horizon and Locality.—Lower Coal Measures (637 feet below the Bedminster Great Vein, and 137 feet above the Ashton Great Vein); South Liberty Colliery, Bristol.

Description.—One wing is partly superposed on the other, and the lower is also partially concealed by shale. The upper wing is represented by a portion of the distal inner portion, and by the wing-apex which is bluntly rounded. The outer margin is broken away, and the original size and shape of the wings cannot be determined.

The manner in which the wing-fragments are exposed on the shale renders systematic analysis of the neuration impossible. All the veins are narrow and sunk in the wing-membrane, while the interstitial neuration consists of transverse nervures arranged at right-angles, and dividing up the various areas into quadrangles. Where forking of the principal veins takes place, the resultant branches first diverge rapidly, and then pass outwards in parallel lines and at right-angles to the margin.

The lower wing-fragment shows a well-defined outer margin, evidently bounded by the costal vein. This margin is regularly and broadly convex, and shows signs of passing proximally into a straight or incurved line. The apex of the wing is narrow and bluntly rounded. The principal veins exposed appear to be portions of the radius, radial sector, and the distal branches of the median.

Affinities.—Fragmentary though these wings are, they nevertheless present features of unusual interest, as they are wholly unlike the blattoid wings found in the South Wales Coalfield, and are as yet the only insect-wings found in the Lower Coal Measures of the Bristol district.

The resemblance in venation and structure to locustid wings is remarkably close. There are the thin, sharply defined branch veins, and the division of the interspaces into rectangular areas by straight transverse nervures; and the texture is quite filmy, apart from the incised veins, as in Locustidæ.

Genus **XEROPTERA**, novum.

Generic Characters.—Wings more than three times as long as wide. Outer margin feebly convex. Subcosta ending far out. Radius reaching almost or to the wing-apex. Radial sector united by commissure to median. Median large, forming two main, equal-sized branches. Cubitus simple. Interstitial neuration of numerous straight cross-nervures.

Xeroptera obtusata, sp. nov. Plate V, fig. 5; Text-figure 26.

Type.—A right fore-wing in counterpart in nodule; British Museum (Johnson Collection, no. I. 1558).

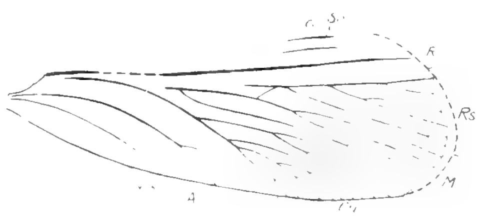

FIG. 26.—*Xeroptera obtusata*, gen. et sp. nov.; diagram of venation of wing, three-halves natural size.—Middle Coal Measures; Coseley, Staffordshire. Johnson Collection, Brit. Mus. (no. I. 1558). Lettering as in Text-figure 16, p. 62.

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

Description.—The wing is not complete, the whole of the outer margin being missing, or hidden by the matrix; the apex is raggedly torn, and much of the

Genus **SCALÆOPTERA**, novum.

Large wings, 60 mm. or more in length. Costa marginal and slightly curved. Subcosta widely separated from margin and giving off straight, oblique and widely-separated branches to the margin. Radius parallel with the subcosta, and giving off the radial sector in the basal half of the wing. Median with few divisions. Cubitus long, with few divisions. Wing feebly plicate. Interstitial neuration forming a fine, close reticulation.

Scalæoptera recta, sp. nov. Plate VI, fig. 1; Text-figure 27.

Type.—Basal half of left wing in counterpart, having a length of 29 mm., and a width of 14 mm.; British Museum (no. I. 13878).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

Description.—The inner margin of the wing is lost or concealed in the matrix,

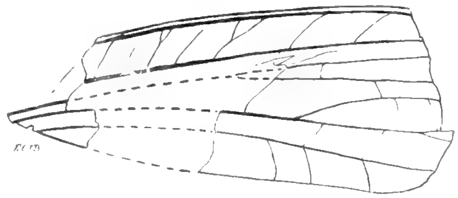

FIG. 27.—*Scalæoptera recta*, gen. et sp. nov.; diagram of the basal half of wing, twice natural size.—Middle Coal Measures; Coseley, Staffordshire. Brit. Mus. (no. I. 13878).

while the anal area, and possibly a part of the cubital area, is missing. A portion of the nodule containing the distal half of the wing is lost. The total length of the wing could not have been less than 60 mm., and judging from its apparent relationships, may have been more.

The surface of the wing is slightly plicated, two low ridges bearing the radius and principal branch of the cubitus, while the subcosta and the median are deeply sunk. Its membranous portion is strongly coriaceous, with stout cross-nervures at wide intervals. The outer margin and the principal veins are feebly spinulose, as best seen on the radius and radial sector. The outer margin is feebly convex, the fairly straight course of the margin, and of all the principal veins, pointing to the wing being much longer than wide; a view also borne out, as we shall see later, by its possible relationships.

The subcosta is widely removed from the margin, parallel with it, and giving off a series of stout branches passing obliquely outwards to the margin. Of these divisions, one only is clearly forked.

Two portions of the radius are present, a short basal portion, and a second piece further out. The vein is separated from the subcosta by an interval less than half that separating the subcosta and the margin. It lies also on a ridge which increases in strength distally. The radius and subcosta are parallel. The actual point of origin of the radial sector is not shown, but can be determined within narrow limits. It arises almost in the basal fourth of the wing, and so far as its course can be traced, diverges from the radius.

The median diverges along its whole course from the radius, and gives off on its outer side two branches, which remain undivided to the broken edge of the nodule. The first branch arises in line with the origin of the radial sector, and at an acute angle which soon enlarges, so that the interval separating it from the radial sector is less than half that separating them at their origin.

The cubitus divides into two nearly equal branches very low down in the base of the wing, the second branch sending off a short division against the broken edge of the nodule.

The stem of the median, and the two branches of the cubitus, have a parallel course, like the outer margin, subcosta and radius, the widening interval between the two groups of veins being occupied by the radial sector, and the two outer branches of the median. The direction of the subcosta, radius, radial sector, and first branch of the median, indicates that they traversed almost the whole length of the wing and ended on the wing-apex. The main stem of the median and the branches of the cubitus would reach the distal half of the inner margin. There are no traces of anal veins.

Affinities.—The extreme width of the intercostal area, the marked divergence of the costa, subcosta and radius from the median and cubitus, are features not readily recognisable among other known fossil insects. The few widely-spaced cross-nervures are not wholly peculiar to the specimen. Similarly, the spinulose principal veins are paralleled by those of *Brodia priscotincta* and *Archæoptilus ingens*. I have not seen so marked a coriaceous texture in any British fossil insect. The length of the wing-fragment before branching of the principal veins occurs, implies a long and relatively narrow wing. Such a wing-form is seen in the Palæodictyoptera and in the Protorthoptera. The wing differs from that of *Brodia priscotincta* in its much greater size, in the presence of a well-developed series of cross-nervures, and in the coriaceous surface of the wing-membrane. The direction of the radial sector and the divisions of the median vein are unlike those in *Brodia*, where these veins curve steadily from their points of origin inwards to the wing-margin.

Two groups of insects described by Handlirsch ('Amer. Journ. Sci.' [4], vol. xxxi, 1911), from the Pennsylvanian Series of the Carboniferous of Mazon Creek, Ill., under the family names of Spanioderidæ and Geraridæ, appear to resemble most nearly the wings we are considering. The wings in these families are long and narrow, and obtusely rounded at the apex, and the principal veins, especially in the Spanioderidæ, pass straight out for the whole, or the greater part, of their length. Their costal area is also broader than the subcostal-radial area, and in both families the interstitial neuration consists of straight cross-nervures, except in the costal area, where they are oblique, as in this specimen.

These resemblances, however, are not sufficient to justify the inclusion of the new wing among the Geraridæ, because they are accompanied by equally or more important differences, such as the spinulose character of the principal veins, the great development of the intercostal area, the marked divergence of the stems of the radius and the median, the coriaceous wing-membrane and the much fewer cross-nervures. The wing, too, possesses quite a leathery texture, while the cross-nervures are broad and flat, forming conspicuous details of the surface.

With our present knowledge, it is only possible to infer that the wing is related to the Geraridæ and Spanioderidæ, that it is a Protorthopteroid, and that it still retains traces of its Palæodictyopteroid ancestry.

Order PROTOBLATTOIDEA, Handlirsch.

The Protoblattoids have a well-rounded head, a prothorax showing little or no expansion, and the wings intermediate in type between those of Palæodictyopteroids and Blattoids. The anal areas of the fore-wings or tegmina[1] are well marked out, and crossed by arcuate or oblique veins reaching the inner margin, while those of the hind-wings are enlarged and marked off from the rest of the wing by an anal fold. The body is more slender than in the majority of Blattoids.

The members of this order form a connecting link between the Palæodictyoptera and the Blattæformes. In many respects there is a close resemblance between the members of the order and those of the Protorthoptera, and the two may have arisen from nearly related stocks.

Genus **PTENODERA**, novum.

Generic Characters.—Subcosta reaching almost to the wing-apex. Radial sector twice furcate; median well divided, with its minor divisions crowded on the inner half of the wing-apex.

I have formed this genus to include a wing-fragment of unusual character in which the principal veins are long, and directed towards the wing-apex with few divisions, and the interstitial neuration consists of straight cross-nervures. The specimen shows that the branching of the principal veins is much similar to that of *Polyetes* among the Protoblattoidea, and to that of *Spaniodera schucherti*, Handl., among the Protorthoptera, in this respect supporting Pruvost, who has established

[1] The thickened rigid fore-wings of Blattoids are usually termed "tegmina."

a sub-order, Archiblattides, to receive many of the insects classed as Protorthoptera by Handlirsch.

The wing is apparently related also to *Scalæoptera recta*, Bolton, and as the latter shows no trace of the formation of an anal lobe, I class this genus with the Protorthoptera rather than with the Protoblattoidea. The Protoblattoidea probably arose from a Protorthopteroid stock.

Ptenodera dubius, sp. nov. Plate VI, fig. 2; Text-figure 28.

Type.—Distal half of a left wing, on the split surface of one half of an ironstone nodule; British Museum (Johnson Collection, no. I. 1559).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

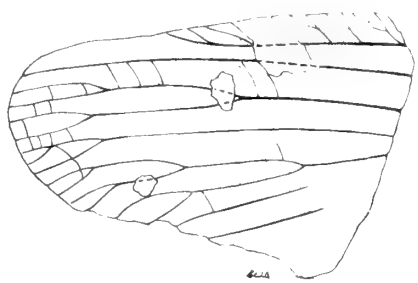

FIG. 28.—*Ptenodera dubius*, gen. et sp. nov.; diagram of apical portion of wing, twice natural size.—Middle Coal Measures; Coseley, Staffordshire. Johnson Collection, Brit. Mus. (no. I. 1559).

Description.—The ironstone nodule has been broken across, and that portion which contained the basal half of the wing has been lost. The distal portion of wing remaining is 27 mm. long, with a width of 16 mm. across the widest part. The width of the basal half of the wing was probably greater.

The distal half of the wing is thin and membranous, and a little wrinkled. The principal veins are well shown, but the interstitial nervures are only clearly visible when the nodule is immersed in water.

The costa is marginal and gradually curves into a well-rounded wing-apex. The subcosta is widely spaced from the costal margin basally, and gradually approaches it as it passes out towards the wing-apex, which it does not reach. It gives off to the wing-margin a series of oblique divisions, several of which fork.

The radius is simple, and passes straight to the wing-apex. Somewhat widely separated from the radius is the radial sector, which must therefore have been given off low down in the base of the wing. It divides into two equal branches, each of which is again equally divided, so that it ends on the middle of the wing-apex in four divisions.

The median vein is large and well branched. The nodule has been broken across just beyond the point of division of the two main branches. The outer branch remains undivided until near the margin, where it forks twice, ending on the inner side of the wing-apex in three divisions. The inner branch forks into two equal twigs, the outer breaking up twice by equal forking into four divisions, while the inner twig forks once. Most of the divisions of the inner branch of the median end on the distal portion of the inner wing-margin.

Two incomplete branches of the cubitus are present, but the character of the vein cannot be determined. No traces of the anal veins are shown.

The principal veins and their main branches are well spaced, and follow the same general direction without being truly parallel. The interstitial neuration consists of fine straight cross-nervures.

Affinities.—The general character of the veins other than the subcosta is seen in several Palæodictyopteroid genera such as *Eubleptus*, but in none that I know are these characters accompanied by a similar type of subcosta. In the oblique, forked divisions of the latter, and the manner in which they are given off, as well as in the course of the subcosta itself, the wing most resembles that of the Protoblattoids, and to this group I would assign it.

INCERTÆ SEDIS.

Genus **PLESIOIDISCHIA**, Handlirsch.

1906. *Plesioidischia*, Handlirsch, Die Fossilen Insekten, p. 346.

Plesioidischia sp. Plate VI, fig. 3; Text-figure 29.

Type.—A fragment of a right wing, 40 mm. long and 10 mm. wide; Manchester Museum (no. L. 4905).

Horizon and Locality.—Middle Coal Measures (binds between "Brooch" and "Thick" coals); Tipton, Staffs.

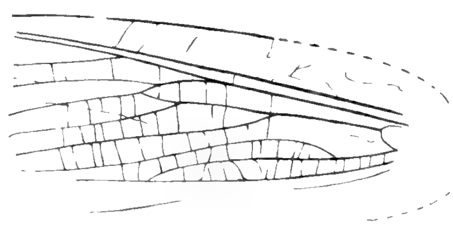

FIG. 29.—*Plesioidischia* sp; diagram of venation of wing-fragment, three-halves natural size.—Middle Coal Measures; Tipton, Staffordshire. Manchester Museum (no. L. 4905).

Description.—The wing-fragment lies on the irregular surface of a small ironstone nodule, the outer costal margin and costal area on one half of the nodule, and the middle portion of the wing on the other. The base and apex of the wing are missing, or still concealed in the matrix. Few definite factors are presented for determination, and the following description is the best we can give.

The outer margin of the wing is formed by the costa, and seems to be curved basally and straight distally. The costal area is widest at the base, and gradually narrows by the approach of the subcosta, which doubtless reached the outer margin far out. The costal area is crossed by a few stout straight branches of the subcosta. The subcosta passes straight from the base to the distal portion of the wing-margin.

The radius is close to and parallel with the subcosta. It gives off two inward diverging branches, the first uniting with the median, but giving off a secondary branch before it reaches the latter. The median gradually diverges from the radius. It gives off two well-marked inner branches, and then bends forwards to join the first branch of the radius. The point of union of the two branches gives origin to a backward twig parallel with the secondary branch of the radius, and with the two inner branches of the median.

The cubitus is represented by a long oblique vein going down to the inner margin. It gives off near its base an outer branch, which curves inwards parallel with the main stem, and reaches the wing-margin much beyond it. The wing appears to have broken along the level of a succeeding vein, but whether this was also a cubital or an anal vein it is impossible to determine.

The interstitial neuration consists of a series of stout strong cross-nervures. The texture of the wing seems to have been membranous.

Affinities.—The chief features of the wing are the strong parallelism of the veins, the numerous and strong cross-nervures, and the unusual mode of union of the radius and median. This assemblage of characters serves to place the specimen in the Protorthoptera, but it is not referable to any known genus, and is too incomplete to justify a new genus for its reception. The nearest approach appears to be *Progenentomum carbonis*, Handl., in which the subcosta reaches the middle of the wing, the radial sector unites with the median, and the interstitial neuration is of straight cross-nervures.

Order BLATTOIDEA.

The most numerous and varied insects found in the Coal Measures are the Blattoids, the recorded forms being classified in several families, embracing nearly 100 genera and 400 species. The early history of their study is dealt with by S. H. Scudder ('Mem. Bost. Soc. Nat. Hist.,' vol. iii, pt. 1, no. 3, 1879), and need not be repeated here.

Notwithstanding the abundance of specimens and forms known, they are insufficient for a satisfactory classification of the group, and do not provide the stages in the life-history of any species. Handlirsch has recorded the occurrence of several egg-cases of Blattoids from the Carboniferous ('Proc. U.S. National Museum,' vol. xxix, p. 716, 1906). Larval forms have been described by Scudder, Handlirsch, Woodward, and especially by Sellards ('Amer. Journ. Sci.' [4], vol. xviii, p. 113, 1904), but in all cases the remains are too incomplete for satisfactory study.

The Coal Measure Blattoids show unmistakably that the race had a much earlier ancestry, as they depart widely from the Palæodictyopteroid type, and have attained a high degree of specialisation. The eggs were enclosed in capsules (Ootheca) much as in modern cockroaches, and the development was by a progressive metamorphosis, in which the rudimentary wings were formed at a relatively early stage, and increased in complexity of structure and size at successive ecdyses. It would also appear that the rudimentary wings were attached to the thorax by broad bases, and that the formation of an articular joint was not developed until the adult stage was reached. The elements of the thorax were as well developed in Coal Measure times as they are to-day, both in structure and function, while the legs, as seen in examples from Commentry (Allier), France, were long, spiny, or covered with stiff hairs, and well adapted for walking or running.

The wings display a remarkable diversity of neuration. The fore-wings are invariably modified by the formation of chitin into stout, horny structures, usually termed "tegmina," which served to protect the more delicate membranous hind-wings concealed beneath them. The costa is always marginal.

The hind-wings are not well known. When found, they are thin, membranous, larger than the tegmina, and folded beneath them. The enlargement of the wing has taken place over the inner half, the costal and radial areas being reduced, and the anal area not marked off from the rest of the wing by a furrow, as is seen in the fore-wings or tegmina. The wide variation in the neuration of the tegmina furnishes the only satisfactory data for classification. Assuming, as we must, that the Blattoids were derived from the Palæodictyoptera, the simplest form of Blattoid must be that in which the wing-neuration most nearly approximates to the latter type. This principle is the basis of Handlirsch's classification.

Modification of the wing-membrane for flight in the case of the hind-wings has brought about, or been accompanied by, a narrowing of the costal and radial areas, a reduction in the strength and extent of these veins, and an increased development of the median and cubital areas, coupled with an increased growth of the wing-membrane inwardly. The hind-wing is, therefore, a much more asymmetrical structure than the fore-wing or tegmen.

The abdomen is broad, somewhat flattened and well-segmented, but no positive evidence is known of an invagination of the terminal segments to carry the egg-capsule. Cerci are present, and Sellards has identified long ovipositors, though this identification is not accepted by Handlirsch.

The habits of Carboniferous Blattoids can only be inferred from those of living forms. I have previously (p. 11) drawn attention to the occurrence of Blattoid wings among the leaves of *Cordaites* bearing numerous shells of the small annelid, *Spirorbis pusillus*, and suggested that the Blattoids frequented decaying vegetation to feed on the *Spirorbis* and similar organisms.

The tegmina of *Phylomylacris mantidioides* occur among masses of the spat ("*Ancylus vintii*") of *Anthracomya phillipsii* in coal shales of the Durham Coalfield. Most of the other Blattoid remains from the Coal Measures of this country have been found in sedimentary deposits in which Ostracods also occur. Apart from these facts, the general faunal associations of fossil insects to which I drew attention on pp. 18—24 are, I think, of great importance, as furnishing definite clues to habits. The same Arthropod-association still persists, and the lagunal and marshy phases of the Coal Measures would furnish a fitting and desirable environment for the whole series.

Classification.—The classification of the Carboniferous Blattoids is difficult, owing to lack of material. The known British forms are few in number, and have been found in several coalfields at horizons which cannot be correlated with each other or placed in a regular sequence.

Scudder's classification does not sufficiently take into account the relationship which undoubtedly exists between the Blattoids and the Palæodictyoptera, and it is based mainly on a knowledge of living forms. For this reason, probably, the Mylacridæ are placed as the first tribe in his group "Palæoblattariæ," in preference to the Archimylacridæ, in which a Palæodictyopteroid relationship is more clearly evident.

Handlirsch's classification gives greater attention to the ancestral type, and is also based on an examination of more numerous specimens than were accessible to Scudder. It is far from satisfactory, and will certainly be much modified when the collection of several thousand Blattoid remains from Commentry is fully worked out by Prof. Meunier, whose results are not yet published. Lameere's general classification ('Bull. Mus. Hist. Naturelle,' 1917, no. 1) is too uncertain to justify adoption.

Dr. P. Pruvost, who has given several years to a close study of the fossil Blattoids of the French and Belgian Coalfields, has modified Handlirsch's classification, and in his latest memoir (1920) he classifies the Blattoidea of Northern France as follows:

BLATTOIDEA.

Family ARCHIMYLACRIDÆ.

Genera *Actinoblatta*, *Manoblatta*, *Archimylacris*, *Asemoblatta*, *Phyloblatta*, *Grypoblattina*, *Archæotiphe*, *Barroisiblatta*, and *Mesitoblatta*.

Family MYLACRIDÆ.

Genera *Hemimylacris, Phylomylacris, Trilophomylacris, Soomylacris, Lithomylacris, Orthomylacris, Stenomylacris.*

Family POROBLATTINIDÆ.

Genus *Premnoblatta.*

This classification seems to accord most nearly with recent discoveries, and is therefore adopted here.

Family ARCHIMYLACRIDÆ, Handlirsch.

Body slender in primitive forms, broadened out in more specialised types. Cerci well developed and jointed. Legs slender and armed with spines. Antennæ slender. Pronotum subcircular. Subcosta distinct, with pectinate or equally spaced branches. Radius well branched, with or without radial sector. Median of one or two main branches. Radius, radial sector and median with outward branches only. Cubitus inwardly curved, and with inward branches. Anal furrow present. Anal area large, extending beyond the basal third of the wing. Interstitial neuration of straight nervures, or an irregular reticulation, or the two combined.

The greater number of Palæozoic Blattoids belong to this family, which is united to the Palæodictyoptera by transitional forms.

Genus **APHTHOROBLATTINA**, Handlirsch.

1906. *Aphthoroblattina*, Handlirsch, Proc. U.S. National Museum, vol. xxix, p. 719, and Die Fossilen Insekten, p. 183.

Generic Characters.—Tegmina two-and-a-half times as long as wide, with convex outer margin. Costal area narrow and strap-shaped. Subcosta extending over two-thirds the wing-length. Radius giving off radial sector near middle of wing, and sending a few simple branches to the apex. Radial sector forking into four or six branches. Median small, with few branches directed inwardly. Cubitus giving off 7—8 branches along its whole length, and extending well out towards the wing-apex. Anal area small.

Aphthoroblattina johnsoni (Woodward). Plate VI, figs. 4, 5; Text-figures 30, 31.

1887. *Etoblattina johnsoni*, Woodward, Geol. Mag. [3], vol. iv, p. 53, pl. ii, figs. 1 *a*, 1 *b*.
1906. *Aphthoroblattina*, Handlirsch, Die Fossilen Insekten, p. 183.

Type.—The pronotum and tegmina in an inverted position with traces of hind-wings on a small ironstone nodule, in counterpart; British Museum (Johnson Collection, no. I. 1067).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, Staffs.

Specific Characters.—Tegmina slightly convex and expanded towards the apex, about two-and-a-quarter times as long as wide. Apex broadly rounded. Costal area occupying three-fourths of the outer margin of the wing. Subcostal vein weak. Radius almost straight and giving off the radial sector about the middle of its length. Radial sector doubly furcate. Median vein widely spaced across the middle of the wing. Cubital vein reaching the inner angle of the wing-apex, giving off outer and inner branches. Anal area large, and crossed by a few small anal veins. Hind-wings thin, larger than the tegmina, and with strong veins.

Description.—The elucidation of the neuration of the wings of the type specimen is difficult, owing to the venation of the hind-wings being impressed

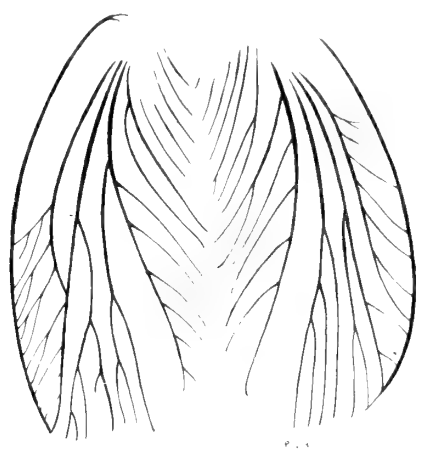

FIG. 30.

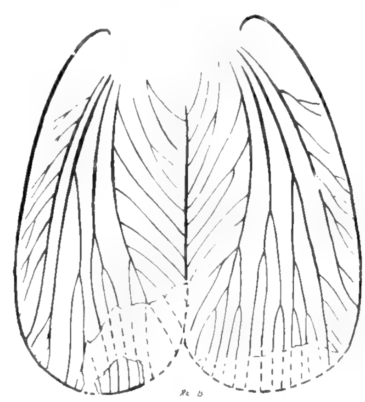

FIG. 31.

FIG. 30.—*Aphthoroblattina johnsoni* (Woodward); diagram of venation of the two fore-wings of the type-specimen, twice natural size.—Middle Coal Measures (binds between "Brooch" and "Thick" coals); Coseley, Staffordshire. Johnson Collection, Brit. Mus. (no. I. 1067).

FIG. 31.—*Aphthoroblattina johnsoni* (Woodward); diagram of venation of the fore-wings of a normal example of the type-series, twice natural size.—Same horizon and locality as Fig. 30. W. Egginton's Collection, "no. 2."

on that of the tegmina. The veins of the hind-wings are stronger than the distal portions of those veins of the tegmina which they overlie. It is probably owing to these factors that the original figures of the type are incorrect.

In both tegmina, as indicated by Dr. Woodward, the median and cubitus are shown as united, whereas this union takes place in the left wing only. Neither of the figures gives an adequate indication of the presence of the hind-wings. In the larger figure the radius and cubitus are represented by a single vein, which is also incorrect. Allusion has already been made to the wings lying on the smaller portion of the nodule in an inverted position. This is demonstrated by the pronotum, which dips under the mesonotum into the matrix, and by the deep impressions of the veins of the hind-wings crossing over, and not under, the veins of the tegmina. The veins of the tegmina are also in relief, instead of being sunken as they normally are on the dorsal surface.

The pronotum has a diameter of 13 mm., and 8 mm. of its length is exposed. The sides curve evenly backwards, and show no sign of flattening, so that its general shape is semicircular. The hinder border is hidden, and disposed at an angle to the surface-plane of the wings. The presence of a sunken, central, pyriform area on the inner surface of the pronotum probably marks the position occupied by the head of the insect. The downward inclination of the front margin of the pronotum, and the elevation of the hinder border, is a frequent feature in the Coal Measure Blattoids.

During life a small gap interposed between the pro- and mesonotum, and this became filled up by sediment on burial in sufficient quantity to cause the pronotum to be lifted from the body of the insect by that half of the nodule which carries the wing-impressions. This inclined position of the pronotum is so common that it appears to have been normal.

The mesonotal area is covered by the anal areas of the tegmina, and its character cannot be determined.

The venation of the right tegmen differs considerably from that of the left. The under surface of the latter is the more nearly perfect, and the venation is more distinct. The costal margins of the tegmina form two broad arcs, sharply bent inwards at the base, and distally merging into the wing-apex. The left subcosta is widely separated from the margin, giving off three oblique branches which fork, the first twice, before reaching the margin. Beyond these branches, the left costa curves inwards and unites with the main stem of the radius at the distal third of the wing. The right costa is more normal, and does not unite with the radius. It gives off six outward branches, of which only the first is forked.

The left radius, after a slight basal curve, passes straight out to the apex, giving off four forward branches, the first forked. This first forked branch appears to be the continuation of the subcosta. The radius of the right tegmen gives off two simple outer branches only.

There is a wide difference between the radial sectors of the two tegmina. That of the left divides in the middle of its length into two equal branches, which in turn fork, the outermost twig forking again, so that the radial sector ends on the margin in five divisions. The right radial sector forks once only beyond the middle of its length, and ends on the margin in only two divisions.

The median in each tegmen is a comparatively simple vein, that of the left being united with the cubitus in the basal fourth, and separating from it at an acute angle. Beyond the middle of the wing it gives off a single forked branch on its outer side. These divisions of the median, with the first branch of the radial sector, occupy the inner half of the apex. The median of the right tegmen is well separated from the cubitus along its whole length, and passes in a bold curve to the inner half of the apex, giving off four simple outer branches.

Apart from its union with the stem of the median, the cubitus of the left tegmen agrees fairly well with its fellow. Both veins curve inwards, and reach the junction of the inner margin with the apex, and both give off 6—7 branches inwardly, the first branch in each case forking.

Which forward branches were given off on the outward side of the cubitus in the left tegmen cannot be made out, but faint furrows on the right tegmen seem to indicate that three simple outer veins were present.

The anal area is long and acutely ovate, extending over nearly a third of the inner margin. Six anal veins are present, the distal one with a strong fork.

The interstitial neuration consists of stout, straight nervures, not always well shown. The inner margin is nearly straight.

The veins of the hind-wings are very fragmentary. They are much thinner than those of the tegmina, and have left a much slighter impress. They appear to consist of a straight costa, separated by a very narrow area from an equally straight subcosta, below which can be made out a portion of the radius, radial sector, and median.

All the veins are widely spaced, and the breadth of the hind-wings must have been about double that of the tegmina.

The dissimilarity between the neuration of the left and right tegmina in the type-specimen suggests a wide varietal range among Coal Measure Blattoids, a feature which needs to be taken into account in the definition of species.

The presence of these abnormalities in the type-specimen somewhat militates against its value for reference, and I therefore add other details from a second example which I received from Mr. W. Egginton. The specific characters given above have been drawn up from this specimen, which lies in a small ironstone nodule, marked "No. 2," having a length of 43 mm. and a breadth of 38 mm. The Blattoid has a total length of 33·5 mm., and a maximum breadth across the tegmina of 24 mm. The inner margins of the tegmina overlap, evidently in their position of rest during life.

The pronotum, apparently in natural position, lies a little out of the horizontal, the front margin dipping downwards, and the hinder margin upwards and a little forwards, so that a slight gap occurs between it and the wings. This feature we have already alluded to, and in this case the pronotum has been carried away as usual, but the wings remain, so that the wing-impressions with the pronotum are on the upper surface of one half of the nodule, the other half carrying the pronotal impression and the wings.

The pronotum is 12 mm. wide and broadly rounded, only a little more than half being visible. It shows a central raised area, oval in outline, and defined from the margins by lateral grooves. The meso- and meta-notal segments show as a low, flat, elongated, heart-shaped region overlain by the anal areas of the tegmina.

Both tegmina are still attached high up on the sides of the body. So far as can be determined through the substance of the tegmina, the hind-wings are attached nearer the middle line, and almost on the upper surface. All four wings are present, the tegmen of the right side being perfect, while that on the left has lost a portion of the inner part of the apex. The right tegmen is 25 mm. long, and 12 mm. wide at its broadest part.

The costal margin is broadly arcuate, and merges into a well-rounded apex. The subcosta is feeble, and gives off 7—10 very oblique branches, each breaking up into numerous twigs before reaching the margin. The intercostal area is wide and strap-shaped, and occupies the greater part of the outer margin.

The radius is well separated from the subcosta at its base, and diverges a little from it along its course. It gives off the radial sector before the middle of the wing is reached, and then passes forward undivided until near the end of the subcosta, where it gives off four or more short oblique branches forward.

The radial sector diverges strongly from the radius, and, like the latter, remains undivided for the greater part of its length. In the last third it gives off two, possibly three, outer twigs, which fork before reaching the margin. The interradial area at the point where the first branch arises is very wide.

The median arises close to the radius, but soon bends strongly towards the inner side of the apex. It gives off three outer parallel branches, the first of which forks.

The cubitus is a powerful and large vein, well apart from the median at its origin, and passing above the middle of the wing in its proximal third, beyond which it curves inwards to the end of the inner margin. It gives off six simple branches and ends in a feeble fork, while two strong branches arise on the outer side and pass to the apex.

The anal area is large, occupying one-third of the margin, and containing six anal veins, the first, second and third forking.

The inner margin is almost straight. The interstitial neuration consists of numerous raised cross-nervures, best seen in the anal and cubital areas. In the radial and median areas the cross-nervures unite laterally and occasionally fork.

Portions of the hind-wings are present, but only the distal branching of the radial sector, median and cubitus is shown beyond the broken end of the left tegmen. The course of the radius and median is traceable across the surface of the tegmen of each side.

The wing-membrane is so thin as to be scarcely discernible.

Aphthoroblattina eggintoni, sp. nov. Plate VI, fig. 6; Text-figure 32.

Type.—Pronotum, tegmina and portions of hind-wings lying on the surfaces of a split ironstone nodule; "No. 1" in the Collection of Mr. W. Egginton.

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

Specific Characters.—Costal margin convex. Cubitus long, strap-shaped, and extending almost the whole length of the outer margin. Radial sector with few simple branches. Median vein forking three times, and ending in middle and inner side of the wing-apex. Cubitus extending the whole length of the inner margin, with no evident outer branches, and feeble forking.

Description.—The specimen is contained in a small greyish-brown nodule, 48 mm. long and 35 mm. wide, and lies with the dorsal surface of the wings and the impression of the pronotum on one half of the nodule, and the wing-impressions and pronotum on the other half. The remains are in good condition, and show a small portion of the head, the pronotum and mesonotum, almost the whole of the left tegmen, and the basal two-thirds of the right tegmen, while a portion of the left hind-wing is disclosed over that area from which the fragment of the

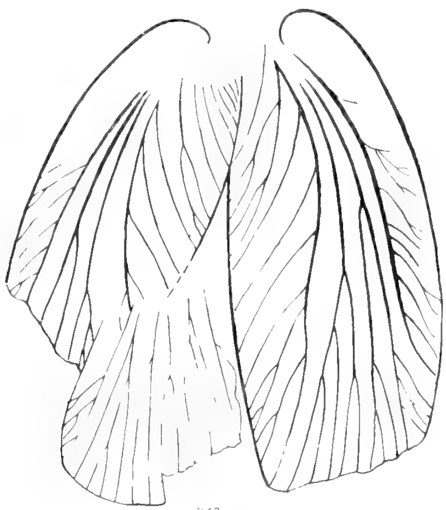

FIG. 32.—*Aphthoroblattina eggintoni*, sp. nov.; diagram of venation of fore-wings and portion of left hind-wing, twice natural size.—Middle Coal Measures (binds between "Brooch" and "Thick" coals); Coseley, Staffordshire. W. Egginton's Collection, "no. 1."

tegmen is missing. That both hind-wings are present is indicated by their principal veins showing in feeble fashion through the tegmina.

The head is small, not more than 3 mm. of its length being visible, and not all of this would be seen were the front margin of the pronotum intact. The latter has been broken away in the middle line, and allows a portion of the head to become visible. The hinder part of the head is well rounded and narrowed, the front being wide, and having a forward and downward slope. It is finely tuberculated. A small aperture in the middle of the head may be due to a loss of matrix.

The pronotum is attached to that half of the nodule which contains the wing-impressions, and the hinder border is still covered with the matrix. Its whole contour cannot be seen, and only the inner surface is exposed. It is semicircular, with a well-defined margin, 12 mm. wide, and 8 mm. long from front to back. The central area has a deep median furrow, and is marked off from the lateral halves by two ridges (representing the furrows on the dorsal surface). These ridges converge anteriorly and almost meet. The inner surface is slightly concave, and indented by three faint furrows on each side, parallel with which are traces of fine striations.

The mesonotum is 4·5 mm. long, and much wider anteriorly than posteriorly. It is convex, and the hinder border has a raised rounded edge. It is strongly chitinous, much more so than the metanotum, which is crushed down beneath the anal areas of the tegmina, only a little of the hinder portion of the left side showing at one point where the anal areas of the wings have been broken away. The right tegmen lies in the position of rest, its inner margin being in line with the axial line of the body. The left tegmen was rotated outwards to a slight degree before entombment—a feature which, combined with the breaking away of its distal third, has enabled the left hind-wing to be better shown. The right tegmen has a length of 33 mm. and a breadth of 13 mm.

The costal margin is moderately thickened, convex, and merges gradually into the wing-apex, the latter bluntly rounded.

The subcostal vein is thin, and encloses a long strap-shaped area, crossed by 9—10 oblique branches, most of them forking twice before reaching the margin.

The radius is a strong vein, nearly parallel with the subcosta, and ending on the outer margin in four small branches, the second only forking. The radial sector arises just before the middle of the wing, diverging but slightly from the radius. It gives off three short outward branches to the apex.

The main stem of the median passes along the middle line of the wing for some distance, and curves inwards to the distal end of the inner margin. The first outward branch arises a little beyond the middle of the wing, and forks into two equal-sized twigs; the remaining two branches remain undivided to the broken edge of the wing. The median and its subdivisions occupy the centre and inner half of the wing-apex.

In the left tegmen the second branch of the median forks. The cubitus is strongly convex in the proximal two-thirds, and bends forwards in the distal third and inwards again to the inner margin. It gives off six inward branches, the fourth and fifth forking before reaching the margin. The anal veins are eight in number, three being very small and short. The first forks twice, and the second once. The inner margin is almost straight. The interstitial neuration is made up of straight nervures. The surface of the tegmina is chitinous.

The hind-wings appear not only to have been covered by the tegmina, when they were in a position of rest on the body, but to have stretched a little beyond them like a fringe.

The left hind-wing is thin and membranous, and marked by numerous veins, the bases still hidden under the tegmen. A little of the distal portion of the costal margin is shown, passing into a very broad and expanded apex. The subcosta reaches nearly to the end of the costal margin, and gives off numerous oblique and forked branches Immediately behind the subcosta is a stout vein with two outer branches, both forking. This vein seems to be the radius. Its basal extension under the tegmen can be traced by a raised line. Behind the radius are two stout veins, each of which forks into equal-sized twigs some distance from the margin. Their position justifies the inference that they unite proximally and join the radius, in which case they must belong to the radial sector. The median is a doubly forked vein. The remainder of the wing is either bent under, or folded upon itself, and further details cannot be made out.

Affinities.—The species differs from *Aphthoroblattina johnsoni* in several important details. The radial sector arises further out, and instead of forking twice, gives off three simple forward veins. The median forks three times, the proximal branch forking again before reaching the wing-apex. In *A. johnsoni* there are two branches, both of which fork. The cubitus vein differs considerably owing to the fact that the main stem divides at the outer third into two branches of equal strength, the outer immediately forking again into two equal twigs, while the inner gives off a small inner twig. No definite outer branches are distinguishable. A strong anal furrow is present, and the first anal vein on both sides divides into three twigs, the remaining 5—6 anal veins being undivided.

Genus **ARCHIMYLACRIS**, Scudder.

1868. *Archimylacris*, Scudder, in Dawson's Acadian Geology, ed. 2, p. 388.

Generic Characters.—Tegmina twice as long as wide, with convex outer margin. Inner margin concave. Radial sector arising in basal half of wing. Anal veins few, anal area large. Neuration of abundant stout straight cross-nervures.

Archimylacris hastata, Bolton. Plate VII, fig. 1; Text-figure 33.

1911. *Archimylacris* (*Etoblattina*) *hastata*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 160, pl. ix, figs. 1—3.

Type.—The greater part of a left tegmen and its counterpart, showing the upper surface; Museum of Practical Geology, Jermyn Street (nos. 24501 and 24502).

Horizon and Locality.—Upper Coal Measures (Gellideg Level of the Mynyddislwyn Vein); near Maes-y-cwmmer, Monmouthshire.

Specific Characters.—Wing broadly elliptical. Costal margin convex; costal area broad at base and stretching beyond the middle of the wing. Subcosta with numerous branches, all oblique. Radius forking twice, and ending near apex of wing. Median branching further out than the radius. Cubitus reaching margin in distal third of wing. Anal veins numerous. Inner margin almost straight.

Description.—A portion of the base of the wing and a considerable part of the apical and inner margin are missing, but the length preserved is 33·4 mm. and its breadth is 16·5 mm.

The wing is strongly outlined, especially along the outer margin, partly owing to a broad concave depression which runs almost the whole length of the subcostal and radial areas, causing the anterior margin to be reflexed dorsally. The inner margin is preserved only along a portion of the anal border, and the inner two-thirds of the wing-apex are also missing. Sufficient is left of the apex to show that it must have been bluntly rounded.

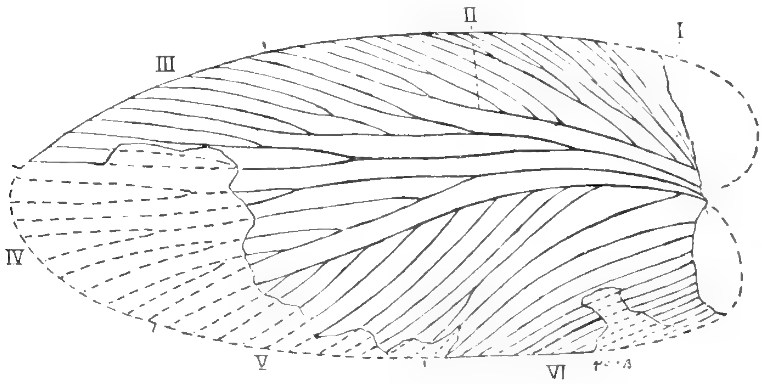

FIG. 33.—*Archimylacris hastata*, Bolton; diagram of venation of left fore-wing, three times natural size.—Upper Coal Measures (Gellideg Level of the Mynyddislwyn Vein); near Maes-y-cwmmer, Monmouthshire. Mus. Pract. Geol. (nos. 24501, 24502). Lettering of veins.—I. costa; II. subcosta; III. radius; IV. median; V. cubitus; VI. anal.

The subcostal vein passes out obliquely from the point of attachment and reaches into the distal third of the wing. It gives off 9—10 very oblique branches, the basal three forking twice, the next two undivided, and the last branch but one forked. The subcostal area is broad basally, and terminates in an acute angle distally.

The actual origin of the principal veins is lost, and the radius appears at its origin therefore to be widely removed from the subcosta. It follows a parallel course to the origin of the first anterior branch, and afterwards diverges, so that it finally ends on the apex of the wing near the middle line. The first branch is important, forking three times in its course and ending in six divisions. The second branch forks only once.

The subcosta and radius together occupy a little less than half the whole wing-area. Dr. Pruvost supposes that a commissural branch unites the radial sector and the median in this species (1919, 'Mémoires pour servir à l'Explication de la Carte Géologique Détaillée de la France,' p. 151), but I cannot perceive this.

The median vein arises in actual contact with the stem of the radius, or is united with it, rapidly diverging to the distal part of the inner margin. Four branches are given off on the outer side, the first forking before the broken edge of the wing is reached. The remaining three probably forked also on the missing part of the wing-apex. The subdivisions of the median occupy the inner half of the wing-apex, and the apex itself.

The regularity of arrangement of the minor veins is a marked feature of this wing, and lends colour to our supposition.

The cubitus gradually diverges from the median along the whole of its course. Ten branches are given off on the inner side, the first only forking.

The anal area is sharply marked off from the rest of the wing by a deep anal groove, the anal area being elevated and somewhat convex in outline. Ten to eleven anal veins can be distinguished, the marginal ones being very short and feeble.

The interstitial neuration consists of close, strong, transverse nervures so numerous as to give the wing-surface a finely corrugated appearance.

The tegmina were apparently of great strength, the unusual development of the transverse nervures adding to the rigidity, while the presence of an oblique ridge served to support and strengthen the radius, median and cubitus at their base, and a similar ridge gave support to the whole of the anal area.

Affinities.—In 1911 (*loc. cit.*) I gave reasons for regarding this species as an Archimylacrid, comparing it with *A. spectabilis*, Goldfuss, and *A. venusta.* More recently, Dr. Pruvost ('Ann. Soc. Géol. Nord,' vol. xli, p. 335, pl. ix, figs. 4—4 *a*, 1912) has expressed the opinion that it is so nearly like *A. belgica*, Handlirsch, and a specimen he has himself described from the roof of the Alfred Vein, Liévin, Northern France, as to be referable to that species. An examination of the figures published by Handlirsch and Pruvost does not support this view. *Archimylacris belgica* was founded by Handlirsch ('Mém. Mus. Roy. Hist. Nat. Belg.,' vol. iii, p. 12, pl. iv, figs. 17—18, 1906) on a wing in the Brussels Museum, from the Westphalian or Middle Upper Carboniferous of Jemappes, Belgium. It was afterwards transferred by him to a new genus, *Parelthoblatta* ('Die Fossilen Insekten,' p. 184, pl. xviii, fig. 54, 1906). This new genus is not accepted by Pruvost, who considers that it is founded chiefly on the pectinate character of the first branch of the radius. He therefore replaces the species in the genus *Archimylacris*, and refers his own specimen to the same genus and species. With this conclusion I cannot agree. Handlirsch's species is characterised not only by the pectinate character of the first branch of the radius, but (and much more important) by the presence of a meshwork of interstitial neuration between the radius, median and cubitus. This latter feature clearly separates not only the French specimen from Handlirsch's genus *Parelthoblatta*, and therefore from *P. belgica*, but the British specimen also; for in both the interstitial neuration consists wholly of a close series of straight cross-nervures, with not the slightest trace of the development of a network.

A. hastata is closely allied to the French species, but the divisions of the main veins are fewer and of a more simple nature. I see no reason to remove the British species from the genus *Archimylacris*, and would refer the French example also to the same genus. This view is now accepted by Pruvost (*loc. cit.*, p. 158).

Archimylacris woodwardi, Bolton. Plate VII, fig. 2; Text-figure 34.

1910. *Archimylacris* (*Etoblattina*) *woodwardi*, Bolton, Geol. Mag. [5], vol. vii, pp. 147—151, pl. xv, figs. 1—1 *a*.

Type.—A left tegmen or fore-wing, 18 mm. long and 10 mm. wide; collection of Mr. D. Davies, F.G.S.

Horizon and Locality.—Coal Measures (a ten-foot shale overlying the No. 2 Rhondda Seam, base of the Pennant Series); Clydach Vale, South Wales.

Specific Characters.—Wing short and broad. Apex well rounded and merging

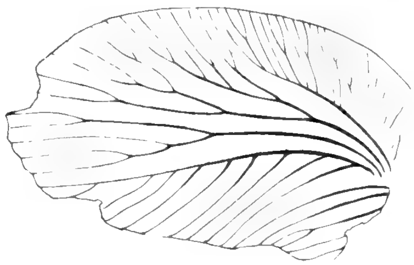

FIG. 34.—*Archimylacris woodwardi*, Bolton; diagram of wing-venation of left fore-wing, three times natural size.—Base of Pennant Series (roof of ten-foot shale overlying the No. 2 Rhondda Seam); Clydach Vale, South Wales. David Davies Collection.

into costal border. Anal area convex. Interstitial neuration of abundant stout cross-nervures, occasionally uniting laterally.

Description.—The tegmen, which is short, broad and strongly chitinous, lies with the convex dorsal surface uppermost. The well-rounded outer margin of the wing merges into the equally well-rounded apex. The inner margin is nearly straight, a slight hollowing only of the middle portion being shown. Notwithstanding its small size, the details of the wing are very clear, the veins and the interstitial neuration being well shown. The basal portions of the main veins are elevated above the surface, the rest of their length and also their divisions being sunk below the general level.

The subcostal vein is weak, and sunk along its whole course. It is widely separated from the costal margin, following a parallel course to beyond the middle of the wing, where it bends outward and joins the margin. The subcosta gives off a numerous series of forked and simple divisions to the costal margin.

The radius arises close to the subcosta and median, diverging from the former in the middle of its length, and approaching it again by the first of the four outer branches which it gives off. The first two branches of the radius are forked, the rest undivided. The radius with its divisions occupies the distal third of the wing-margin. At the junction of the basal and middle thirds of the wing, the radius gives off a strong radial sector which diverges from it, giving off two outer branches, the first forking twice into four twigs. The radial sector occupies the outer half of the wing-apex.

The median curves regularly inwards along its whole course, reaching the inner end of the wing-apex, and giving off three outer branches, of which the first is forked. With its subdivisions it occupies a much less area than any other main vein.

The cubitus follows a course nearly parallel with the median, and gives off nine inward branches. With its subdivisions, it occupies almost the whole of the distal two-thirds of the inner margin.

The anal area is strongly convex, and crossed by at least five anal veins, the third being forked.

The interstitial neuration is well developed in the neighbourhood of the subcosta, and consists of a close-set series of straight cross-nervures. These are in relief, and in places seem to unite laterally, and to cross the main veins.

Affinities.—The wing is typically Archimylacrid. At the time of its discovery in 1910 I was unable to show that it possessed a close relation to any known species, but more recently Dr. Pruvost has recorded a very similar example, *A. atrebatica*, Pruv., from the Coal Measures of Bruay, Northern France.

The presence of a well-defined radial sector is a Palæodictyopteroid feature which most Blattoids have lost, and stamps the species as primitive. It is therefore interesting to find that Pruvost draws special attention to the fact that *A. atrebatica*, Pruv., is the oldest Archimylacrid of the Northern French Coal Measures, being found in the lower portion of the Formation of Bruay, over the vein Ernestine at Lens, in a shale containing seeds and drifted plant-remains.

Archimylacris incisa, sp. nov. Plate VII, fig. 3.

Type.—Pronotum, mesonotum, and the basal portions of the tegmina in an ironstone nodule; British Museum (Johnson Collection, no. I. 15900).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, near Dudley, Staffs.

Specific Characters.—Wing robust. Principal veins widely spaced. Interstitial neuration of stout cross-nervures, which unite in a meshwork in the wide areas.

Description.—These Blattoid remains are 21 mm. long. The pronotum lies with its underside uppermost on that portion of the nodule which also bears the impressions of the under surfaces of the tegmina, while the impression of the underside of the pronotum and the fragments of the tegmina upside down occur on the other half. The hinder margin of the pronotum is still hidden in the matrix, and the impressions of the under-surfaces of the wings would need to be destroyed to expose it.

The pronotum is semicircular in outline, so far as can be determined. The inner surface is marked out into two lateral areas which join in front of, and behind, the central area, the latter being hollow, probably to lodge the head of the insect during life. The central hollow of the pronotum is crossed in front and behind by close-set parallel wrinkles, while a suture-like crack traverses the whole structure in the middle line. Posteriorly to the central hollow, the lateral halves have separated and become wrinkled up against each other.

The condition of the pronotum shows that it was convex, the central hollow of the inner surface marking off an area which was more convex than the sides, and separated from them by grooves which bent round and joined behind the central more elevated area. The central area is thinner than the sides and infolded.

Lying behind, and partially overhung by the hind border of the pronotum, is a heart-shaped structure, irregularly indented, owing its superficial appearance to the overlap of the anal areas of the wings on it. On one side of this structure can be seen what appears to be part of a stout segment, having a thickened anterior border, and a convex surface bearing a few low tubercles. The central indented structure occupies the position of the mesonotum, and the lateral stouter segment may be a part of it, or of the metanotum which has been pushed forward.

The base of the left tegmen is in actual articulation with what I suppose to be the mesonotum. As the tegmina lie with their under surface uppermost, the impressions on the opposite half of the nodule are also of the same surface.

The fragment of the left tegmen is largest, and in the best condition, but not more than a third of it is present. The tissue is thickly chitinous, much more so than that of the pronotum.

The costal margin is convex, and the costal area strap-shaped and wide. Seen from the underside it appears smooth, a few diagonal wrinkles alone crossing the surface. We may therefore infer that the divisions of the subcosta are weakly incised on the upper surface.

The subcostal vein is more convex in direction than the margin, the costal area being widest at the base.

The radius arises close to the subcosta, and gradually diverges from it. It shows no divisions in the basal portions preserved.

The median vein arises even closer to the radius than does the latter to the subcosta, and bends inwards in a convex curve for some distance, afterwards flattening and becoming parallel with the radius.

The cubitus arises closer to the anal furrow than to the median, but bends outwards in a bold sweep away from it, becoming almost parallel with the median. It gives off three inward branches in the part preserved, the first low down near the base, and the remaining two at wide intervals further out. The course of the main stem is such as to indicate that it reached the distal portion of the inner margin, so that the wing-apex was wholly occupied by the divisions of the radius and the median.

The anal veins seen are five in number, the first forking twice and the rest single. They probably occupied the proximal third of the inner wing-margin.

The articulation of the tegmen to the mesonotum seems to have been strengthened by the formation of three ridges, two formed by the deepening of the bases of the subcosta and radius, and a third by a similar thickening just inside the anal furrow, which in this specimen coincides with the line of the first branch of the cubitus.

The basal part of the subcostal area shows a deep hollow; this feature is seen in several of the British Blattoids, and favours the assumption that while the point of attachment lay immediately behind, the frontal part of the mesonotum developed an area which served as a fulcrum for the tegmina.

The right tegmen is represented only by the base of the costal border and subcosta, short portions of the radius, median, a part of the cubitus with two proximal branches, and the inner anal vein dividing into three.

The interstitial neuration consists of strong cross-nervures, frequently uniting laterally, and on the broader areas forming a slight open meshwork.

Affinities.—Fragmentary though the wing is, it yet shows many of the features of *A. venusta*, Scd., having the same wide costal area, the same relation of subcosta, radius and median so far as these can be traced, and the cubitus beginning to branch low down before the radius and median show any trace of branching. The interstitial neuration in both consists of straight cross-nervures occasionally uniting laterally.

This wing is more robust than that of *A. venusta*, Scd., and the anal veins are more oblique in direction. The whole of the main veins and those of the anal area are more widely spaced. In its robust character the wing approaches *A. acadica*, Scd., but in that species the interstitial neuration does not unite laterally.

Archimylacris (Schizoblatta) obovata, Bolton. Plate VII, fig. 4; Text-figure 35.

1911. *Archimylacris (Schizoblatta) obovata*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 157, pl. vii, figs. 4—6.

Type.—The distal two-thirds of a left tegmen, having a length of 23 mm. and a greatest breadth of 10 mm.; Museum of Practical Geology, Jermyn Street (nos. 24506 and 24507).

Horizon and Locality.—Base of the Upper Coal Measures (Gwernau Level of the Mynyddislwyn Vein); Maes-y-cwmmer, Monmouthshire.

Specific Characters.—Costal border moderately convex, and passing into a subacute apex. Costal area narrow and strap-shaped. Subcosta extending just beyond the middle of the wing. Radius large, much divided, and occupying the distal portion of the outer margin, and the outer half of the apical margin and apex. Median a small vein with few divisions ending on the inner apical margin. Cubitus occupying the whole of the inner margin beyond the anal veins. Surface covered with a close series of oblique wrinkles.

Description.—When I first described this specimen in 1911, I was of opinion that the length of the complete wing was not more than 25 mm. With a larger knowledge of the structure and form of the Blattoid tegmen I should now estimate the length at nearer 35 mm., the complete structure being a little over two-and-a-half times as long as broad.

The costal border is broadly convex, more so in the distal than in the proximal half.

The subcostal area is narrow, the subcosta being a delicate vein, sending a number of forked and simple branches obliquely to the costal margin. Probably half of the subcosta is missing, though three branches of it are present. One

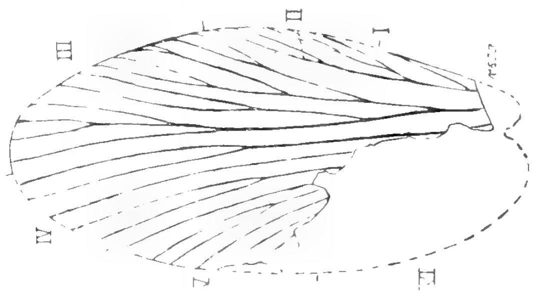

FIG. 35.—*Archimylacris* (*Schizoblatta*) *oborata*, Bolton; diagram of venation of left fore-wing, three times natural size.—Upper Coal Measures (Gwernau Level of the Mynyddislwyn Vein); Maes-y-cwmmer, Monmouthshire. Mus. Pract. Geol. (nos. 24506, 24507). Numbering of veins as in Text-figure 33, p. 104.

remains single, the next gives off a simple basal twig, and forks just before reaching the margin, while the outer branch is undivided.

The radius is much the largest of the principal veins, and is widely separated from the subcosta over the middle portion of its length. Before reaching the middle of the wing it divides into two diverging branches, each of which forks, and afterwards gives off a series of smaller veins, eleven in number, which occupy the distal outer margin, and the outer half of the wing-apex.

The median vein is not complete, and seems to consist of a main stem, giving off a long branch in the basal third of the wing, a second branch in the middle, and a final branch in the outer third. The first branch only divides, so that the median ends on the inner apical margin in five divisions.

The remaining marginal veins are probably wholly cubital. They are five in number, one only forking.

There is no trace of the anal portion of the wing, or of the remainder of the cubitus.

The wing is thick, coriaceous in texture, and convex dorsally. The whole surface is covered by a dense series of irregular oblique wrinkles. In some places a close-set series starts out from the sides of a vein, and dies out in the interspace. In other places sets of wrinkles are interrupted by smooth interspaces, this arrangement occurring at haphazard. There are a few cases in which the wrinkles unite.

Affinities.—There can be no doubt as to this specimen representing an Archimylacrid. Dr. Handlirsch, who makes *Archimylacris* the type of a family, Archimylacridæ ('Proc. U.S. National Museum,' vol. xxix, p. 722, 1906), has also founded a new genus, *Schizoblatta*, and with the type-species of this genus the specimen here described is in close agreement.

The points to which I attach importance are the following: In both, the subcostal area extends for a short distance beyond the middle line, the veins in each case passing out obliquely to the margin. A very wide interval separates the stem of the subcosta from that of the radius in the middle of their length, and this area is narrowed distally in each case by the approach of the marginal veins. The radius is a large and much branched vein, and separates into two main divisions, which fork at the same level and reach the apical point of the wing—in this specimen just beyond it. The median is relatively small, while the cubitus has few branches, passing obliquely out, like those of the subcosta, to the margin.

The anal area in the type, *Schizoblatta alutacea*, is long, attaining nearly half the length of the wing. In the specimen here described this part is missing, as is also a part of the cubitus. The missing portion of the inner margin extends beyond the middle of its length, and knowing how frequently the anal vein determines the line of fracture, this extended broken area becomes significant.

Dr. Handlirsch's definition of the genus *Schizoblatta* is as follows: "Front wing elliptical, about two and two-fifth times as long as broad. Costal area extending about three-fifths the length of the wing, with about nine or ten normal veins; not expanded at the base. Radius divided into two principal stems, the superior of which separates into six branches and the inferior into eight, the majority of the latter ending in the apical border. The median likewise divides into two main stems, the anterior of which forms five branches, and the posterior four, all of which fuse in the apical margin. The eight branches of the gently vaulted cubitus take up the entire inner border. The anal area attains nearly half the length of the wing. Cross-veins area not to be distinguished, but instead there is a fine-grained leathery structure" (*loc. cit.*).

If the genus is to be maintained apart from that of *Archimylacris*, I would base the characters on the obliquity of the marginal veins of the subcosta and cubitus, the presence of a wide interval between the former and the radius, and the wide area occupied by the latter.

The division of the radius into two unequal branches, with its symmetrical double bifurcation, is also, I venture to think, a feature of primary importance.

In the wide divergence of the radius and median, this species agrees with Scudder's genus *Spiloblattina*; but in this case the veins do not converge again to enclose an elongated or oval area.

Archimylacris, sp. indet. Plate VII, fig. 5.

1911. *Archimylacris*, sp. indet., Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 163, pl. x, fig. 3.

Type.—A fragmentary wing, lacking the apex and the base; Museum of Practical Geology, Jermyn Street (no. 24503).

Horizon and Locality.—Base of Upper Coal Measures (Gellideg Level of the Mynyddislwyn Vein); near Maes-y-cwmmer, Monmouthshire.

Description.—The specimen is much too fragmentary for any attempt at specific determination. A portion of the distal margin is present, with three branches of the subcosta. These are succeeded by eight straight veins, two at least forking, which belong to the radius and median series. These are followed by an equal number of veins partially hidden by the surface of the integument, which is much wrinkled over this area. These, I assume, are parts of the cubitus vein. The wrinkling of the integument over the cubital area is very marked.

The special interest of this wing-fragment is in its association with portions of a leaf of *Cordaites*. Scudder and others have commented on the general association of the wings of Blattoids with leaves of *Cordaites*, but have not, so far as I am aware, drawn attention to a feature which is well shown by this leaf, namely, pits on its surface. I have repeatedly found such depressions on the leaves of *Cordaites* in the Lancashire Coalfield, and in many cases seen the hollows occupied by the shells of *Spirorbis pusillus*. The shallow pits on the *Cordaites*-leaf associated with this fragmentary wing show faint traces of a spiral, similar to the impression of *Spirorbis*, and such shells were, I think, once attached to it. While the Carboniferous Blattoids may have been wholly phytophagous, we are led by our knowledge of the living Blattids, especially by the common cockroach (*Periplaneta orientalis*), to assume the contrary, and to regard them as more likely to have been omnivorous, in which case the association of Blattoid remains with the leaves of *Cordaites* bearing the sedentary *Spirorbis* is easily understood. The association also lends support to the belief that the Blattoids were semi-aquatic in habit, or lived in marshes and swamps in which decayed vegetation formed a home for *Spirorbis*.

Archimylacris, sp. indet. Plate VII, fig. 6.

1911. *Archimylacris*, sp. indet., Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 152, pl. vii, fig. 2.

Type.—Impression of basal portion of left tegmen; Museum of Practical Geology, Jermyn Street (no. 24508).

Horizon and Locality.—Base of Upper Coal Measures (Mynyddislwyn Vein, Gellideg Level); near Maes-y-cwmmer, Monmouthshire.

Genus **PHYLOBLATTA**, Handlirsch.

1906. *Phyloblatta*, Handlirsch, Bull. U.S. Nat. Mus., vol. xxix, p. 738.

Generic Characters.—Tegmina elliptical, two-and-a-quarter to two-and-a-half times as long as wide; costal area strap-shaped, rarely wide, and extending usually to three-fifths or two-thirds the length of the wing; not expanded basally. Radius with numerous branches, all of which reach the outer margin. Median with outer branches only, reaching wing-apex. Cubitus large, much branched, and occupying distal two-thirds of inner margin. Anal area large with numerous veins. Interstitial neuration rugose leathery or much cross-wrinkled.

Phyloblatta sulcata (Bolton). Plate VIII, fig. 1; Text-figure 36.

1911. *Gerablattina (Aphthoroblattina) sulcata*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 165, pl. viii, figs. 1—3.

Type.—Greater part of tegmen and its counterpart impression showing the under surface only; Museum of Practical Geology, Jermyn Street (nos. 24504 and 24505).

Horizon and Locality.—Base of the Upper Coal Measures (Gwernau Level of the Mynyddislwyn Vein); near Maes-y-cwmmer, Monmouthshire.

Specific Characters.—Costal area broad; subcosta strap-shaped, and extending far out. Radius with six branches, occupying outer half of wing-apex. Median with few divisions and occupying a small area of the wing. Cubitus united with median at the base. Anal furrow well developed. Anal veins 5—8.

Description.—The specimen comprises the greater part of a right tegmen, showing the under surface, the counterpart impression being on a second piece of black shale. An irregular narrow fringe of the wing-membrane has been lost along the outer and inner margins, and the inner half of the wing-apex is also missing. The length of the fragment is 35 mm., and the greatest width 16 mm., the perfect wing being probably about 45 mm. long, and 22—23 mm. wide. If this estimate is correct, the wing is short. Tegmina are usually at least two-and-a-half times as long as wide. The structure is well preserved, and the principal veins and their subdivisions are in relief.

The costal margin is thickened, strongly convex, and well rounded at the base. The costal area is unusually broad and strap-shaped, extending over two-thirds of the costal margin. The basal portion of the costal area is smooth, and not crossed by branches of the subcosta.

The subcosta is thin, elevated basally, and somewhat crenulated, doubtless owing to post-mortem change or pressure. The subcosta is parallel with the costal margin over more than one-half the length of the wing, and gives off six oblique branches to the margin. Three of these branches are forked.

The radius passes out to the apex of the wing, giving off six outer branches, the first forking once, and the second twice before reaching the margin. The

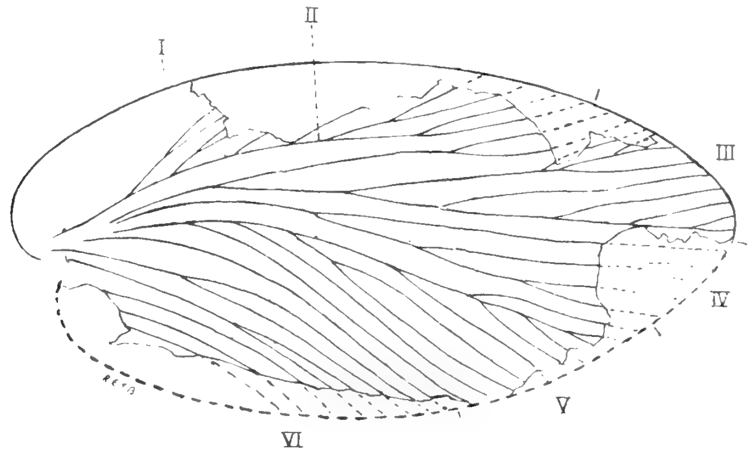

FIG. 36.—*Phyloblatta sulcata* (Bolton); diagram of the venation, and restored outline of fore-wing, two-and-a-half times natural size.—Upper Coal Measures (Gwernau Level of the Mynyddislwyn Vein); near Maes-y-cwmmer, Monmouthshire. Mus. Pract. Geol. (nos. 24504, 24505). Numbering of veins as in Text-figure 33, p. 104.

remaining branches are undivided. The radius and subcosta together occupy a little less than half the total wing-area.

The median vein is convex outwards in its basal half, and then bends inwards to the junction of the inner and apical margins. It gives off three long, outward, undivided branches, all of which are parallel with the main stem of the radius. Basally, the median curves sharply inwards and unites with the cubitus, the two veins having a very short common stem.

The cubitus is the largest and most important vein in the wing, although but faintly outlined at the base, where its union with the median is nevertheless quite clear. It gives off seven inwardly directed branches, the third only forking. On its outward side two branches are given off.

The anal furrow is represented by a strong ridge, and is therefore a well-marked groove on the dorsal surface of the wing. The anal area is large, extending at least one-third the length of the inner margin, and crossed by five anal veins, the first and second only being forked. The whole of the anal area is not shown, and 3—4 veins may be missing.

The interstitial neuration consists of a close series of transverse nervures or wrinkles, it is impossible to say which. They are best seen in the anal and cubital areas.

Affinities.—The union of the stems of the median and cubitus veins, the occupation of the greater part of the inner half of the wing by the median, whose branches take up the whole of the inner margin outside the anal area, and the strong parallelism of the branches of the principal veins, are well-marked features which in the main agree most, I think, with *Phyloblatta*. Its resemblance to *Gerablattina* is also marked, and it is well to remember that Handlirsch has referred several species originally placed in the latter genus to *Phyloblatta*. This question of the generic relationship is a good example of the difficulty of allocating species to genera whose characters are not wholly known.

Phyloblatta transversalis, Bolton. Plate VIII, fig. 2; Text-figure 37.

1917. *Phylloblatta transversalis*, Bolton, Proc. Birmingham Nat. Hist. Phil. Soc., vol. xiv, pp. 100—103, pl. vii, figs. 1, 2.

Type.—Remains of two Blattoids, consisting of the tegmina, two pronota, and portions of the hind-wings, in a split nodule of ironstone, 60 mm. long, and 45 mm. broad; Geological Museum, University of Birmingham.

Horizon and Locality.—Coal Measures; Staffordshire.

The nodules were collected by Dr. Blake and agree in all respects with those found at Tipton and Coseley, Staffordshire, in the binds between the "Brooch" and "Thick" coals of the Middle Coal Measures.

Specific Characters.—Radius relatively simple with five branches, radial sector large and evenly forked; median vein small, with three outer branches; cubitus vein long with seven inward branches; anal area small with few anal veins.

Description.—The remains of three insects are shown on the split surfaces of two small ironstone nodules. The larger nodule contains the remains of two Blattoid tegmina, two pronota, and fragments of hind-wings. One tegmen is almost complete, while of the other more than half is shown, the distal end having been lost in splitting the nodule.

The tegmina lie with the under surfaces uppermost, the impression of the underside being preserved on the larger portion of the nodule. As both are from the left side, it follows that they belong to two insects—a conclusion confirmed by the presence of a pronotum in close association with each. In the case of the more nearly complete tegmen, the pronotum lies a little apart, and upside down, like the tegmen, while the pronotum of the more incomplete wing lies on the basal portion of the tegmen itself, and has the dorsal surface uppermost. Traces of hind-wings are present, lying on a slightly lower plane than the tegmina, and showing only the underside.

As the two tegmina are specifically identical, the more nearly complete example has been taken as the type and is here described in detail.

The tegmen has a length of 32 mm., and, as a small part of the apex is missing, its total length must have been about 35 mm. The width is uniform over the basal half of the wing, and averages 11·5 mm.

The costal margin forms a strong convex curve, in this respect contrasting with the inner margin, which is nearly straight. The wing-apex is directed backwards owing to the great convexity of the costal margin. The whole wing has a broad semilunate appearance.

The subcosta is a feeble vein, not easily discernible; its outwardly-directed twigs pass out obliquely, and are twice or thrice forked. Like the main stem, they are faintly impressed, and cannot be traced up to the costal margin. Eight twigs can be determined. The subcostal area is strap-shaped, and extends beyond the middle of the wing.

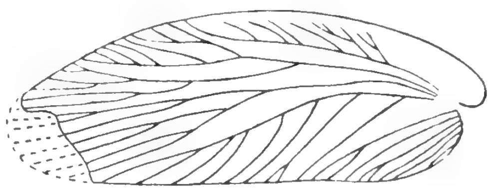

FIG. 37.—*Phyloblatta transversalis*, Bolton; diagram of venation of left fore-wing of type-specimen, twice natural size.—Middle Coal Measures; Staffordshire. Geol. Mus. Univ. Birmingham.

The radius is a strong vein, and shows an inner sub-division which has all the characters of a radial sector. Basally, it seems joined to the median, but it is an apparent junction only, the wing-base being pressed in upon itself, and bringing the two close to one another. After giving off the inner (radial sector) branch, the radius gives off five outer branches which reach the distal third of the outer margin. The first of these branches seems to break up into three twigs, but the structure of the wing is not clear at this point. The radial sector, which arises in the basal half of the wing, forks at the distal third into two equal branches, the outer forking twice into four divisions, and the inner forking once. The radius and radial sector occupy the whole of the outer half of the wing-apex.

The median vein diverges from the radius along its whole course, and reaches the distal end of the inner margin, giving off three outer branches in the distal half of the wing. These pass straight to the apex, the first forking twice, and the second once, the third remaining undivided to the broken edge of the wing. The branches of the median occupy the whole of the inner half of the wing-apex.

The cubitus remains above the middle line of the wing in the basal third, curving inwards and flattening in the outer two-thirds of the wing, and giving off seven inward branches, the second alone forking low down near the margin.

The anal area is small, and crossed by six oblique anal veins, the first and third of which fork.

The interstitial neuration consists of a close-set series of straight cross-nervures which unite laterally as they cross the wider areas.

The pronotum in close apposition with this wing has its inner surface uppermost. This shows a central shallow concave area, bounded by two lateral ridges, which die away as they approach the hinder border. The general outline is broadly circular.

The second tegmen is much less exposed than the first, and has its apex buried under the second pronotum. So far as its structure can be determined, it agrees with the wing already described.

The second pronotum has been crushed, the anterior border being turned round upon the base of the wing, and partly broken away. The posterior margin is almost straight, and that of the anterior well rounded.

Traces of two hind-wings are shown, one a little in advance of the more nearly complete wing, and partly underlying it, and the other underlying the costal and radial areas of the second incomplete wing. The first hind-wing shows a portion of the distal extremity, with a series of incomplete veins, probably belonging to the radius, median, and cubitus; the remains of the second hind-wing probably consist of the distal radial twigs only.

Affinities.—The distinguishing features of the tegmina are essentially those of *Phyloblatta*, unless we except the interstitial neuration. This is composed of straight cross-nervures, which unite laterally across the wide areas between the main stems of the radius, median, and cubitus, but not producing anywhere a meshwork such as is usually seen in the Phyloblattids.

Handlirsch doubts the presence of a cross-neuration in the genus *Phyloblatta* (' Proc. U.S. National Museum,' vol. xxix, p. 731, 1906), but there seems no reason why it should not be present in the more archaic members of the genus, as they all have an Archimylacrid ancestry, in which a cross-neuration is a dominant feature.

The species is closely allied to a form figured as *Gerablattina* sp. by Brongniart (' Insectes Fossiles des Temps Primaires,' pl. xlvi, fig. 7, 1893), and repeated by Handlirsch (' Die Fossilen Insekten,' pl. xxx, fig. 35, p. 295, 1906) under the name of *Blattoidea*, sp. Handlirsch regards Brongniart's specimen as belonging either to the Spiloblattinidæ or to the Archimylacridæ. Unfortunately the interstitial neuration is not shown. If, as in these specimens, Brongniart's species possesses a cross-neuration, or one in which the nervures unite laterally, it must be referred to *Phyloblatta*.

(Archimylacridæ) kirkbyi (Woodward). Plate VIII, fig. 3.

1887. *Lithomylacris kirkbyi*, Woodward, Geol. Mag. [3], vol. iv, p. 55, pl. ii, figs. 4*a*—4*b*.
1887. ? *Hermatoblattina kirkbyi*, Scudder, Proc. Bost. Soc. Nat. Hist., vol. xxiii, p. 357.
1906. (*Archimylacridæ*) *kirkbyi*, Handlirsch, Die Fossilen Insekten, p. 238, pl. xxiv, fig. 37.

Type.—Left wing (tegmen); formerly in the collection of the late Mr. James Kirkby.

Horizon and Locality.—Upper Coal Measures (bed No. 33); near Meithil, coast of Fifeshire.

Description.—Our knowledge of this wing depends on the description and figures published by Dr. H. Woodward. His description is as follows: "Outline of wing pointed-ovate, slightly flattened on its superior border; length of wing 15 mm., breadth 8 mm. The 'mediastinal' [subcostal] vein occupies rather more than a fourth of the entire area of the wing; it extends to about two-thirds of the length, where it unites with the superior margin of the wing; it branches six times; one of these branches has three forks. The 'scapular' [radius] vein extends nearly to the extremity of the wing; it remains single for over one-fourth of its length, and then branches into three veins, the middle one of which is again forked. The 'externo-median' [median] vein continues parallel to the scapular vein for a slightly longer distance before it branches at the extremity of the wing into three inferior veins, two of which are again forked. The 'interno-median' [cubitus] vein occupies about one-fourth the entire area of the wing; it gives off three almost equidistant branches, none of which appear to be forked. The anal vein is nearly straight, and has three other almost parallel oblique simple veins occupying the anal area."

Affinities.—Neither Woodward's figures nor the later modified drawing published by Handlirsch are very helpful in enabling us to identify the genus. Handlirsch has reversed the figure given by Woodward, and shows three veins which may belong to the subcosta, a radius with three forward branches, and a well-divided median ending on the wing-apex in nine outer branches. Woodward's "mediastinal" becomes the cubitus, and no anal veins are shown. This seems a more reasonable interpretation of the wing.

Woodward's comparison of the wing with *Lithomylacris pittstonianum*, Scd., is unfortunate, as in that species the radius is a large, much-branched vein, occupying nearly half the outer margin, while the radius (scapular) in *A. kirkbyi*, Woodw., has three divisions only as shown by him, although it is a more branched structure when the figure is reversed and the veins reconsidered, as by Handlirsch.

In the absence of the type-specimen, it is not possible to do more than refer the species to the family Archimylacridæ.

BLATTOIDS INCERTÆ SEDIS.

Remains of Blattoids have been found at four horizons and in four localities in the Kent Coalfield. They were obtained from small cores, the edges of which had cut through the wings, and rendered them so fragmentary as to be useless for the determination of genera or species. They serve, however, to indicate that the Kent Coal Measures may eventually prove to be as rich in fossil insect-remains as the Coal Measures of the Pas-de-Calais. The depths of the cores given with the original description of these fossils were found afterwards to have been reckoned from a private datum, while the depths now given have been corrected to Ordnance datum.

Phyloblatta (?), sp. Plate VIII, fig. 4.

1912. *Phylloblatta* (?), sp., Bolton, Quart. Journ. Geol. Soc., vol. lxviii, p. 321, pl. xxxiii, figs. 3, 4, 5.
1915. *Phylloblatta* (?), sp., Bolton, Trans. Inst. Min. Eng., vol. xlix, p. 45.

Specimen.—Impression of a Blattoid wing, 5 mm. long and 2·5 mm. wide; Museum of the Kent Coal Concessions Company, Dover.

The impression is that of the middle part of the margin of a tegmen. This may be a part of the outer margin, as I formerly supposed, but I now think it more likely to belong to the inner margin, and to show branches of the median and cubitus veins.

Horizon and Locality.—Shales at a depth of 1967 ft. in the Maydensole boring, Kent Coalfield.

Phyloblatta (?), sp.

1912. *Phylloblatta* (?), sp., Bolton, Quart. Journ. Geol. Soc., vol. lxviii, p. 321, pl. xxxiii, figs. 8, 9.
1915. *Phylloblatta* (?), sp., Bolton, Trans. Inst. Min. Eng., vol. xlix, p. 45.

Specimen.—Impression of part of a Blattoid wing, 6 mm. long and 3 mm. wide; Museum of the Kent Coal Concessions Company, Dover.

The fragment appears to belong to the proximal part of the wing, and shows a long vein giving off six branches.

Lying more inward are the remains of a short forked vein.

Horizon and Locality.—Shales at a depth of 954 feet in the Ripple boring, Kent Coalfield.

Blattoid Wing-Fragment. Plate VIII, fig. 5.

1912. "Blattoid," Bolton, Quart. Journ. Geol. Soc., vol. lxviii, p. 321, pl. xxxiii, figs. 6, 7.
1915. "Blattoid," Bolton, Trans. Inst. Min. Eng., vol. xlix, p. 45.

Specimen.—Impression of a wing-fragment 3 mm. long and 2·25 mm. wide; Museum of the Kent Coal Concessions Company, Dover.

The fragment shows a little of a well-curved margin and three veins, one with a small fork on the wing-margin. The curvature indicates that the fragment belongs to the apical end of the wing.

Horizon and Locality.—Black shale at a depth of 2180 feet in the Barfreston boring, Kent Coalfield.

Blattoid Wing-Fragment. Plate VIII, fig. 6.

1915. "Blattoid," Bolton, Trans. Inst. Min. Eng., vol. xlix, pp. 45, 46, pl. ix, fig. 24.

Specimen.—Distal portion of a tegmen, including the whole of the wing-apex; Museum of the Kent Coal Concessions Company, Dover.

Portions of the subcosta, radius, and median veins can be determined. The subcosta is represented by a little of the main stem which sends off four simple branches to the outer margin. The radius divides low down into two branches, the outer dividing again into two nearly equal twigs, which pass out to the outer margin of the wing. The inner branch divides into four twigs, all reaching the apical margin. The cubitus is represented by a long vein, giving off a series of eight to nine inward branches.

Horizon and Locality.—Shales at a depth of 2424 feet in the Stonehall boring, Kent Coalfield.

Family Mylacridæ, Scudder.

1879. Scudder, Mem. Bost. Soc. Nat. Hist., vol. iii, pt. 1, no. 3, p. 40.
1906. Handlirsch, Die Fossilen Insekten, p. 258.

Fore-wings variable in shape, but generally broad and short, nearly always widest at the base. Costal area more or less triangular. Subcosta with branches arising in a radial manner. Radius sending numerous branches outwardly, or dividing into two widely dividing branches. The median either gives off its branches serially, or forms two compound main branches. Cubitus with a variable number of inward branches. Anal area large, with the anal veins usually ending on the inner margin (Handlirsch).

Scudder established this family for a numerous series of North American Blattoids, all of which are characterised by the subcostal area being widened out basally, and the subcostal vein and its branches reduced from the strap-shaped form seen in Archimylacrids to a shorter structure, in which the branches arise mainly from the root of the vein, and radiate in fan-fashion into the subcostal area.

The humeral portion of the subcostal area is usually smooth, and destitute of subcostal branches, or where these are present, they are short and do not reach the margin. Owing to the enlargement of the subcostal area, the point of attachment of the wing becomes central, instead of being in front of the wing-axis as in the Archimylacridæ. The principal veins and their branches show a greater tendency to pass straight outwards to the wing-margin than in the Archimylacridæ, while the pronotum has become broader and shorter, and assumes more of a reniform appearance.

The wing-surface is leathery and coriaceous, and often cross-wrinkled. Pruvost states that the interstitial neuration is composed of a fine network of nervures, which is more correct, the thickened wrinkled condition being a later development. The body is broad and flat.

Handlirsch regards the Mylacridæ as an early, extremely developed, lateral branch of the Blattoid series, and thus still retaining rather primitive characters, best seen in the median vein. Handlirsch adds (1906, 'Proc. U.S. Nat. Mus.,' vol. xxix, p. 766): "Perhaps they owe their origin to an adaptation to their environment, for it is remarkable how similar many of them are to certain leaves of ferns, with which they are generally found (a fact to which Scudder had already drawn attention). Probably they lived under deciduous fern-fronds, and by their similarity to the pinnæ were protected from their enemies."

Pruvost (1920) considers that the Mylacridæ may constitute a well individualised phyletic series which sprang late from the Archimylacrid stock. He divides the family Mylacridæ into two divisions, Hemimylacridian and Mylacridian, the former, as typified in *Phylomylacris* and *Hemimylacris*, being really intermediate forms lying between the true Archimylacrids and the true Mylacrids (Mylacridians), and more nearly descended from the first. Pruvost also points out that Handlirsch has placed *Apophthegma* (the *Hemimylacris* of Saxony) with the Archimylacridæ, and the American members of the *Hemimylacris* among the Mylacridæ. He is somewhat uncertain whether to place the Hemimylacridians with the Archimylacridæ or with the Mylacridæ, but decides in favour of the latter, suggesting that both the Hemimylacridians and the Mylacridians are of polyphyletic origin.

Genus **HEMIMYLACRIS**, Handlirsch.

1906. *Hemimylacris*, Handlirsch, Proc. U.S. Nat. Mus., vol. xxix, p. 767.

Generic Characters.—Wings twice as long as wide. Costal area broad, in one species almost triangular, in another somewhat strap-shaped. Radius with four outer branches, the first dividing into two or three twigs. Median with three branches directed inwards. Cubitus with 4—5 branches which do not occupy the whole of the free inner margin. Anal area two-fifths the length of the wing, and more than twice as long as wide.

Handlirsch remarks that this genus may be classed almost as well with the Archimylacridæ as with the Mylacridæ, thus agreeing with Pruvost.

Hemimylacris obtusa, Bolton. Plate VIII, fig. 7; Text-figure 38.

1911. *Hemimylacris obtusa*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 154, pl. x, figs. 4, 5.

Type.—A stout right tegmen, lying on a surface of fireclay full of Stigmarian rootlets, and distorted by pressure; Museum of Practical Geology, Jermyn Street (no. 24510).

Horizon and Locality.—Upper Coal Measures (Four-foot Seam of Swansea); Gladys Colliery, one mile east-south-east of Penller-gaer Church, Glam.

Specific Characters.—Costal margin convex; subcostal vein dividing by repeated forking into five twigs; costal area triangular. Radius with a radial sector, the latter much divided. Median with a few forked inward branches. Cubitus large, with four branches, the second twice forked. Anal area wide, and crossed by numerous veins, the first giving off a simple branch, and then dividing twice by equal forking. Inner margin almost straight.

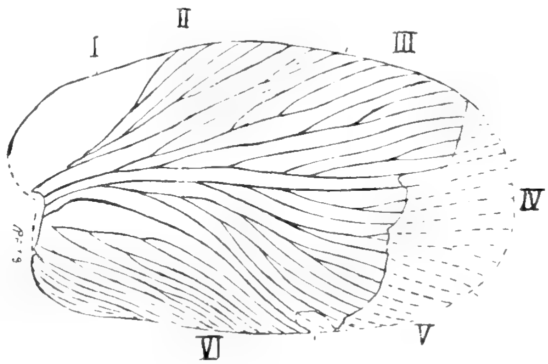

FIG. 38.—*Hemimylacris obtusa*, Bolton; diagram of right fore-wing with apex restored, three times natural size.—Upper Coal Measures (four-foot Seam of Swansea); Gladys Colliery, near Penller-gaer Church, Glamorganshire. Mus. Pract. Geol. (no. 24510). Numbering of veins as in Text-figure 33, p. 104.

Description.—A short rounded right tegmen, 23 mm. long and 14 mm. wide, broken across the basal third along the anal furrow, and the apex missing.

The subcostal area is broadly triangular, the subcostal vein sunken, and passing out obliquely, giving off a basal branch which forks into two equal twigs, the most distal twig forking again. A single undivided branch is given off near the end of the subcosta.

The radius gives off a strong radial sector, and afterwards sends outwardly three simple branches. The radial sector sends four branches to the margin, the first forking twice, and the fourth once, the second and third being simple.

The median vein appears to give off the stem of the cubitus near its base, but this appearance is probably due to the crumpling of the tegmen. The first of the three inward branches of the median arises further out than any of the divisions of the radius or cubitus. The first branch divides into three twigs, and the second forks on the broken edge of the wing. All the branches pass straight out towards the wing-apex.

The cubitus is convex in its basal half, and straightens out distally, giving off four inward branches, the second dividing into three, and the fourth forking. The divisions of the cubitus occupy the distal half of the inner margin.

The anal area is large, and marked off from the rest of the wing by a deep anal furrow. The first anal vein breaks up into five divisions, by a triple forking, and the second forks twice. The third anal vein forks near its base, and the remaining 3—4 veins appear simple. The anal veins end on the margin in at least fourteen twigs.

The interstitial neuration cannot be determined.

Affinities.—The mode of branching of the subcostal vein, the presence of a decided radial sector and the character of the first anal vein, are features which would justify the inclusion of this species in the genus *Soomylacris*, were it not for the fact that the median is not divided into two equal branches. There is a close correspondence between this species and *H. ramificata*, Handl., and I therefore retain it in the genus *Hemimylacris*, although, as I have stated elsewhere, I am inclined to merge the two genera into one, as marking a transitional group between the Archimylacridæ and the Mylacridæ.

Hemimylacris convexa, Bolton. Plate VIII, fig. 8.

1911. *Hemimylacris convexa*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 156, pl. vii, fig. 3.

Type.—Proximal half of a tegmen lying on an irregular surface of black shale; Museum of Practical Geology, Jermyn Street (no. 24512).

Horizon and Locality.—Pennant Series (Shales associated with the Graigola Seam); Clydach Merthyr Colliery, Clydach Valley (Swansea Vale), Glam.

Specific Characters.—Costal area triangular. Radius with a well-defined radial sector, the two occupying most of the outer margin and the outer half of the wing-apex. Median small. Cubitus arcuated and ending on the middle of the inner margin, and outer third of the apex. Anal veins few.

Description.—Only the proximal half of the tegmen is shown, and this does not exceed 10 mm. in length. The subcostal area is much crushed and broken, and but two branches of the subcostal vein can be seen on it.

The radius arises in the middle of the base, and at once divides, evidently giving off a radial sector. The radius shows two marginal veins, while the radial sector sends off a long branch towards the wing-apex, the branch forking near the broken edge of the wing.

The median vein is represented by a portion of the main stem, which forks twice.

The cubitus has an arcuated stem bifurcating twice into four branches. Three anal veins can be distinguished.

Affinities.—The fragmentary and crumpled condition of this wing makes its elucidation difficult and unsatisfactory. The chief features distinguishable are the almost equal costal and anal areas, the presence of a radial sector, and the origin of several anal veins arising from one stem. Few though these characters be, they are sufficient to refer the specimen to the Mylacridæ, and to the genus *Hemimylacris*.

Genus **PHYLOMYLACRIS**, Pruvost.

1919. *Phylomylacris*, Pruvost, Faune Continent. Terr. Houill. N. France (Mém. Explic. Carte Géol. France), p. 199.

Generic Characters.—Tegmina semi-ovate, with rounded apex. Surface coriaceous, with a fine close meshwork of interstitial nervures giving a shagreen-like appearance. Wing-attachment in middle of wing. Costal area triangular. Subcostal branching, partly pectinated and partly radial, extending beyond the middle of the wing. Radius well developed. Median with numerous branches. Cubitus large and well branched. Anal area large, convex, and crossed by numerous anal veins.

Pruvost has formed this genus to include certain Blattoids found in recent years at Lens and Liévin in northern France. They possess a superficial resemblance to the type-species of *Necymylacris*, *N. heros*, Scd., but their differences are nevertheless so marked as to justify the formation of a new genus. Pruvost in the work in question placed Goldenberg's *Blattidium mantidioides* in the genus *Archæotiphe*, having at the time only the original drawings of Kirkby to rely on. After borrowing the type-specimen, I came to the conclusion that Goldenberg's species must be referred to a new genus, in which I also placed *Necymylacris villeti*, Pruv., *N. lafittei*, Pruv., and *N. godoni*, Pruv. To this new genus I proposed to attach the name of my French friend, Dr. P. Pruvost, and intimated my intention to him, at the same time sending my manuscript. I received a reply and the proof-sheets of his new work, in which it appeared that he also had recognised that the three species previously referred to *Necymylacris* must be placed in a new genus, to which he had already given the name of *Phylomylacris*. Our conclusions were identical as to the generic value of his species, and as his work antedates my own, I am unable to attach his name to the new genus, but must adopt the generic name of *Phylomylacris* for the British species.

Had Dr. Pruvost received my photographs and drawings earlier, he would not have referred *B. mantidioides* to the genus *Archæotiphe*, but to *Phylomylacris*, as he based the characters of the latter on the same details of structure as I had determined for the genus in which *B. mantidioides* should be placed. The fact that we arrived at the same conclusion, and by the selection of the same structures, has been a satisfaction to both.

Phylomylacris mantidioides (Goldenberg). Plate IX, fig. 1; Text-figure 39.

1867. *Blatta* or *Blattina*, Kirkby, Geol. Mag., vol. iv, p. 388, pl. xvii, figs. 6, 7.
1877. *Blattidium mantidioides*, Goldenberg, Fauna Saræpont. Foss., vol. ii, p. 20.
1879. *Etoblattina mantidioides*, Scudder, Mem. Bost. Soc. Nat. Hist., vol. iii, p. 72, pl. iii, fig. 6.
1906. (*Archimylacridæ*) *mantidioides*, Handlirsch, Die Fossilen Insekten, p. 237, pl. xxiv, fig. 27.
1919. *Archæotiphe mantidioides*, Pruvost, Faune Continent. Terr. Houill. N. France, p. 170.

Type.—Basal half of left tegmen in nodule; Kirkby Collection, Hancock Museum, Newcastle-on-Tyne.

Horizon and Locality.—Upper Coal Measures (zone of *Anthracomya phillipsii*); South Hylton, opposite Claxheugh on the Wear, Durham.

Specific Characters.—Surface of wing coriaceous. Costal margin convex; subcosta feeble, with few simple branches passing obliquely to the margin. Costal area acutely pyriform. Radius much divided, and occupying outer half of wing-apex Median with numerous divisions, and passing to inner half of wing-apex.

FIG. 39.—*Phylomylacris mantidioides* (Goldenberg); diagram of venation of type, a left fore-wing, three-and-a-half times natural size.—Upper Coal Measures (zone of *Anthracomya phillipsii*); South Hylton, opposite Claxheugh on the Wear, Durham. Hancock Mus., Newcastle on-Tyne (Kirkby Coll.).

Cubitus large, extending to the distal end of the inner margin, and giving off five or more inner branches, the first and third dividing. Anal area tumid, anal furrow well defined. Anal veins 9—10 in number, the first forking twice, and also sending three weak branches forward. Inner margin convex, but less so than costal margin.

Description.—The surface of the nodule surrounding the wing-fragment is covered with the "spat" or young fry of a species of mollusc to which Kirkby gave the name of *Ancylus vinti*, but which I have since shown to be the young fry of *Anthracomya phillipsii* ('Trans. Inst. Mining Engin.,' vol. xlix, p. 675, 1915); also Trechmann and Woolacott ('Geol. Mag.' [6], vol. vi, p. 207, 1919).

The wing-fragment, measuring 13·5 mm. long and 8 mm. wide, is in excellent condition, and lies with the dorsal surface uppermost. The whole of the venation is well marked. Kirkby's original figure is not correct, and his errors have been repeated by Scudder and Goldenberg. Goldenberg did not describe the species he named, and Scudder, to whom we owe the first detailed account, was hindered by the faulty drawing, and does not seem to have seen the specimen. Handlirsch removed the species from *Etoblattina*, regarding the specimen as an indeterminable form of the Archimylacridæ. Re-examination of the type-specimen shows errors in the earlier descriptions and figure, and I now re-describe and re-figure the type, placing it in the new genus established by Pruvost.

The wing is a stout structure, with a coriaceous surface which has enabled it to be perfectly preserved. The costal margin is well rounded inwardly at the base, and flattens over the middle of the wing. Assuming that it agreed with wings of a Phylomylacrid type, the margin would gradually merge distally into a broadly rounded apex.

The subcostal vein is the weakest of the whole series, and passes obliquely outwards, reaching the margin about the middle of the wing. It gives off five undivided branches which are oblique in direction, and fail to reach the margin.

The costal area is broad basally, and ends in an acute angle against the margin. It may be best described as pyriform.

The radius is a powerful vein, giving origin, in the inner third of the wing, to what seems to be a well-marked radial sector, and dividing into two equal branches a little further out. The outer of the two distal branches divides by twice forking into three twigs, which may have reached the middle of the outer margin. The inner of the two branches forks once only.

A wide area separates the radius from the subcosta over the greater part of its length, the widest interval being at the point where the radius divides into two main branches. The branch (? radial sector), of which but few divisions are shown on the wing-fragment, diverges inwardly from the main stem of the radius into the middle of the wing, giving off two branches, the first forking close to the broken edge of the nodule. From its position the ultimate divisions must have ended upon the outer half of the wing-apex, and the distal part of the outer wing-margin.

The various divisions of the radius are so divergent that they enclose a considerable portion of the whole wing, while they are equally well spaced out from the subcosta in front, and the median behind. The base of the radius stands up in relief, and owing to a little enfolding of the wing, overhangs the bases of the median and cubitus, but does not unite with them.

The median vein arises close to the radius, and like the latter, bends inwards at the base in a strong curve, which is continued until the direction is obliquely inward, when it becomes straightened.

At the summit of the basal curve the median sends off a short oblique vein inwards to the cubitus. This vein is a distinct commissure, and not an enlarged interstitial nervure. The significance of this commissural vein is not yet fully understood. Pruvost has recorded a similar structure in species of the genus *Archimylacris* (*op. cit.*, p. 151), and mentions that Scudder and Handlirsch have also indicated its occurrence in other forms. It is not, however, present in *Archimylacris woodwardi*, Bolton, and *A. hastata*, Bolton.

The median remains undivided in the proximal third of the wing, and then forks, the inner of the resultant veins again dividing on the broken edge. The areas on either side of the main stem of the median are, like those of the radius, well spaced.

The cubitus vein is less curved basally than the median and radius, well separated from the latter, and passing obliquely towards the distal end of the inner margin of the wing. It gives off six inward branches, the first arising near the base, and margins the anal furrow. The second branch gives off two irregular twigs which do not reach the margin, and the fourth is forked. The rest are undivided.

The whole of the anal area is remarkably well developed. It stands out as a tumid mass, marked off from the rest of the wing by the first branch of the cubitus, and with all the anal veins in high relief.

A broad area interposes between the first anal vein and the anal furrow, and upon this run out a few small and wavy veins which die out on the membrane. The first well-defined vein has a short stem dividing at once into two equal branches, which continue to the margin. The inner of these two branches either forks again, or has received the larger and distal portion of the next vein, the basal part being joined to the third vein, and forming an enclosed area. The next vein forks, and also the sixth, the remainder being closely packed together, and rapidly diminishing in strength and length as they crowd down upon the margin.

The interstitial neuration consists of a well-defined meshwork which shows a tendency to a longitudinal arrangement in the direction of the wing-margin.

Affinities.—The incorrect figure published by Kirkby has been a source of confusion, and probably accounts for Goldenberg's reference of the species to *Blattidium*, Scudder. At the time when he so referred it, Scudder had become familiar with the distinctive characters of wings of this type, and had created a new genus *Necymylacris* to receive them ('Mem. Boston Soc. Nat. Hist.,' vol. iii, p. 52, 1879). We can only account therefore for his reference of the wing to *Etoblattina* on the score of the faulty drawing, as he does not seem to have seen the wing. The later drawing by Handlirsch is wrong in almost every detail, and his reference of the wing to the Archimylacridæ was the only one possible under the circumstances.

Scudder's genus *Necymylacris* was founded, not upon *N. lacoana*, as Handlirsch assumes (a fragment only of that wing being known), but upon *N. heros*. Handlirsch's later name of *Eumorphoblatta* ('Die Fossilen Insekten,' p. 195, 1906) is rightly reduced by Pruvost ('Ann. Soc. Géol. Nord,' vol. xli, p. 350, 1912) to the position of a synonym.

The figures of the three new species published by Pruvost in that paper are admirably reproduced, and as they show a complex of raised nervures in nearly all the areas of the wings, such as is seen in the British specimen, and as the species agree among themselves while differing from the type of Scudder's genus *Necymylacris*, I considered them to represent a new genus, as already mentioned. In *N. heros* Scudder plainly shows an interstitial neuration of closely-packed transverse nervures, which he describes as "a minute tracery of nearly straight, very closely approximated, excessively delicate, scarcely impressed, cross-lines."

Apart from this difference, there is a close relationship between *Necymylacris* and Pruvost's *Phylomylacris*. Regarding, as I do, the character of the interstitial neuration, especially when well developed, as one of more than specific importance, I consider that *Phylomylacris* is a valid genus.

Genus **SOOMYLACRIS**, Handlirsch.

1906. *Soomylacris*, Handlirsch, Die Fossilen Insekten, p. 260.

Generic Characters.—Wings short and wide, being two to two-and-a-half times as long as wide. Costal area broadly triangular, the subdivisions of the subcosta arising from a central point, the inner branches only reaching the costal margin after a very oblique course. Radius with distinct radial sector. Median dividing low down into two main branches, while the cubitus is long, with simple or forked branches. Anal area large, nearly as long as the subcostal area, strongly convex, and crossed by numerous anal veins, the first usually thrice divided, both the subcostal and anal areas extending nearly to the middle of the wing.

Soomylacris deanensis (Scudder). Plate IX, fig. 2; Text-figure 40.

1895. *Etoblattina deanensis*, Scudder (in part), Bull. U.S. Geol. Surv., no. 124, p. 34, pl. xii, fig. 1.
1896. *Etoblattina deanensis*, Scudder, Geol. Mag. [4], vol. iii, p. 12, fig. 1.
1906. *Soomylacris deanensis*, Handlirsch, Die Fossilen Insekten, p. 260, pl. xxvii, fig. 15.

Type.—Right tegmen, lower view, lacking apical portion; U.S. National Museum, Washington (Lacoe Collection, no. H. 2132*b*; Nat. Mus. no. 38090).

Horizon and Locality.—Coal Measures; Foxe's Bridge, Forest of Dean, Gloucestershire.

Description.—Scudder described and figured two specimens from the Forest of Dean under the name of *Etoblattina deanensis*, but the second is dealt with in this monograph under the new specific name of *Soomylacris stocki* (see p. 130).

The type tegmen of *S. deanensis* has a length of 25 mm., and a maximum breadth of 13 mm. across the anal area. Scudder gives the length as 38 mm., but the wing has lost a second portion of the apical end since he figured the specimen. The anal area is broken, and has become slightly displaced along the line of the anal furrow, but to so slight an extent as not to hinder measurement.

The costal margin is strongly convex basally, becoming almost straight over the middle of the wing, in this respect differing from *S. stocki*, which is increasingly convex in the middle of the wing—a fact noted by Scudder. The inner margin is more nearly straight, and the wing narrows as the apex is reached, the maximum width being across the anal area.

The subcosta is made up of three main branches, the first forking into two equal twigs, the second forking twice into three twigs, and the third forking three times into four twigs. The subcostal area is very wide basally, and terminates in an acuminate angle beyond the junction of the first and second thirds of the wing.

The radius is a powerful vein dividing low down into two main branches, the outer breaking up into four twigs by a trifid forking, while the inner branch forks into two, and each of these into two again, the two twigs of the inner secondary fork each dividing into two. The radius thus ends on the broken edge of the wing in ten twigs.

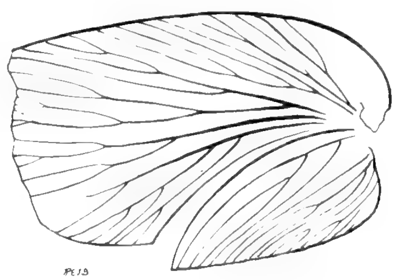

Fig. 40.—*Soomylacris deanensis* (Scudder); diagram of venation of right tegmen (the diagram reversed), twice natural size.—Coal Measures; Foxe's Bridge, Forest of Dean, Glos. U.S. National Museum, Washington (Lacoe Coll., no. H. 2132 *b*; Nat. Mus. no. 38090).

The median vein forks into two main branches at about the end of the proximal third of the wing. The outer branch divides into two equal twigs, the inner forking again further out. The inner branch forks once only on that portion of the wing which is now preserved, although Scudder has figured it as breaking up into six ultimate twigs by repeated forking of the innermost of the two branches now seen. Scudder shows twelve twigs of the median ending on the inner half of the wing-apex, while the actual specimen now shows only five. Scudder is wrong in showing a twig coming off inwardly from the first main division of the median, and dying out in the wing-membrane. The appearance is due to a slight furrow on the impression. This furrow can be traced across the branches of the adjoining cubitus.

The cubitus, like the median, is sigmoidally curved, and gives off five inward branches, and ends upon the distal end of the inner margin in a small fork. The second and third branches of the cubitus fork twice, and end on the margin in three twigs each.

Unlike the rest of the wing, which is flatly convex, the anal area is well rounded, and must have projected somewhat above the general surface. It is crossed by six anal veins, the first being a large structure breaking up into four branches, and more widely separated from the anal furrow proximally than is its outer branch distally. The second vein is simple. The third forks twice, and ends in three twigs. The fourth and fifth fork once each. Traces of two more anal veins are seen on the margin.

The interstitial neuration can only be distinguished clearly in the anal area, and consists of irregular cross-nervures which cross the main veins and unite laterally to form a meshwork, which is not, however, of a strictly reticulate character.

Soomylacris stocki, sp. nov. Plate IX, fig. 3; Text-figure 41.

1895. *Etoblattina deanensis*, Scudder (in part), Bull. U.S. Geol. Surv., no. 124, p. 34, pl. xii, fig. 3.
1896. *Etoblattina deanensis*, Scudder, Geol. Mag. [4], vol. iii, p. 12, fig. 2.
1906. *Soomylacris deanensis*, Handlirsch, Die Fossilen Insekten, p. 260, pl. xxvii, fig. 16.

Horizon and Locality.—Coal Measures; Crump Meadow, Forest of Dean, Gloucestershire.

Type.—Fragments of two tegmina; U.S. National Museum, Washington (Lacoe Collection, no. H. 2132 *c*; Nat. Mus. no. 38090).

Description.—The fragment of a left tegmen has lost much of its base and apex, while the greater part of the anal area is obscured by the anal area of the presumably opposite right tegmen. It lies with the under-surface uppermost, the anal area of the second tegmen being right side uppermost. Feeble traces of what appear to be a hind-wing can be distinguished through the fragment of tegmen, and project a little beyond its margin at one point. The specimens are on a dark grey shale in which occur numerous remains of *Neuropteris*, *Annularia*, etc.

The outer margin is seen on the displaced shoulder of the wing, and on the portion of the outer half of the wing that remains. It is more convex than in *S. deanensis*, and the shoulder bends inwards almost at a right-angle, that of *S. deanensis* being regularly rounded.

The subcosta is represented by the bases of three stout veins which spring from the same point, all showing forking, and by two straight veins running out on the costal margin on the fragment. These two seem to be the terminals of the innermost forking seen on the shoulder of the wing. The intercostal area is broader than that of *S. deanensis*. The base of the radius is missing, and the union of the two twigs into which the outer branch divides is missing. Each of these twigs forks again half-way between its origin and the margin.

The inner branch of the radius divides by twice forking, and the inner of the resultant twigs forks again, so that the radius ends on the margin in at least nine twigs.

The median forks equally twice, the inner of the four twigs again forking twice into three.

The cubitus is a simpler structure than that of *S. deanensis*. It consists of a sigmoidally curved main stem giving off five inward branches, the first and third only forking. The cubitus, therefore, ends on the inner margin in eight twigs, that of *S. deanensis* in eleven.

The anal area of the right tegmen is superficially much like that of *S. deanensis*, but the first anal vein gives off three branches in place of two, the innermost forking. In *S. deanensis* the middle branch forks. The second vein forks twice, that of *S. deanensis* being undivided; the third forks once into two twigs, that of *S. deanensis* having three; the fourth forks once, the fifth is undivided, and the sixth forks twice into three twigs. Traces of a seventh vein are present. Portions of the anal area are shown near the inner margin, and above the outer edge of the anal area of the right wing, but they are too fragmentary to determine the course of the veins.

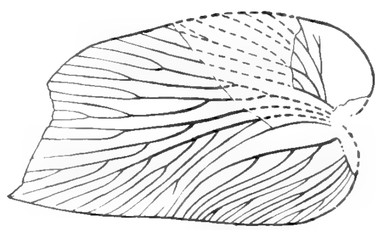

FIG. 41.—*Soomylacris stocki*, sp. nov.; diagram of venation of two tegmina, twice natural size.—Coal Measures; Crump Meadow, Forest of Dean, Glos. U.S. National Museum, Washington (Lacoe Coll., no. H. 2132 *c*; Nat. Mus. no. 38090).

The inner margin is almost straight, and owing to the greater convexity of the outer margin, the wing appears to have been narrower apically than *S. deanensis*.

The interstitial neuration is similar to that of *S. deanensis*. Traces of possibly one of the hind-wings can be seen underneath the costal margin and under the outer twigs of the radius. The wing is closely related to that of *S. deanensis*, but the differences, especially in the cubitus, are sufficient to distinguish the two.

Soomylacris burri, Bolton. Plate IX, fig. 4; Text-figure 42.

1912. *Soomylacris (Etoblattina) burri*, Bolton, Quart. Journ. Geol. Soc., vol. lxviii, p. 318, pl. xxxiii, figs. 1, 2.

Type.—Left tegmen; Museum of the Kent Coal Concessions Co., Dover.

Horizon and Locality.—Coal Measures (dark shale from a depth of 1208 feet); Barfreston Boring, Kent.

Specific Characters.—Subcosta with few divisions. Radius with well-marked radial sector, which is well developed and much divided. Median with two main divisions. Cubitus large, with six simple branches. Anal area very wide basally, and with 4—6 veins. Tegmen tapering along both margins to the apex.

Description.—The tegmen lies with the under surface uppermost, lacking only a small portion of the wing-apex. It is short and broad, measuring 14 mm. long and 8 mm. wide. The dorsal surface is convex, the exposed under surface being concave.

The costal margin is rounded, especially in the basal portion of the subcostal area. Distally the margin curves into the wing-apex, which is bluntly rounded. The inner margin curves outwards in its distal half, so that the wing is widest basally, and narrows into the wing-apex.

The subcosta is a strong vein with few branches, the first two being simple, and passing out obliquely. A forked branch arises further out, and near the margin of the wing a single simple branch. The costal area is broad basally, and well rounded.

The radius is a large, much-divided vein, occupying, with the subcosta, the outer half of the wing. It is short, and gives off a radial sector in the basal

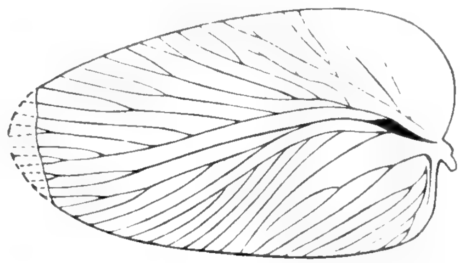

Fig. 42.—*Soomylacris burri*, Bolton; diagram of venation of left tegmen, four times natural size.—Coal Measures (dark shale from a depth of 1208 ft.); Barfreston Boring, Kent. Mus. Kent Coal Concessions Co., Dover.

fourth, afterwards passing out obliquely to the outer margin, and giving off four outward branches, the first irregular in its course, and with two feeble twigs which do not reach the margin, the second and third forking well out, and the fourth small and undivided. The radial sector passes straight to the wing-apex, giving off six strong branches, the first, second, and fourth forking, the rest remaining undivided.

The median is convexly curved basally, and bent inwards to the inner margin. It gives off a strong forward triple-divided branch in the basal fourth, and further out a second branch, which forks three times into four branches. The eight divisions of the median end on the distal third of the inner margin and part of the apex.

The cubitus describes a regular sigmoidal curve, and gives off at regular intervals a series of six inwardly directed branches, all of which are undivided.

The anal area is very wide basally, and crossed by 4—6 veins, the first forking twice, the second once, the third undivided, and the fourth forked. Traces of two very small anal veins are also seen in the curve of the wing-margin. The anal area is strongly convex between the anal furrow and the first anal vein.

The interstitial neuration of the anal area appears to consist of straight cross-nervures. Over the rest of the wing the interstitial neuration cannot be made out.

Affinities.—When first describing this species, I regarded it as closely allied to forms which Handlirsch has placed in his genus *Hemimylacris.* There can be no doubt, from what has been already said, that a close relationship exists. Pruvost (*op. cit.*, pp. 222—4) has recorded two species of *Soomylacris* from the Lens and Liévin Coalfields of Northern France, *S. liévinensis*, Pruv., and *S.* aff. *deanensis.* The occurrence of these British species may serve to indicate the Westphalian affinities of the Kent and Forest of Dean Coalfields.

Genus **ORTHOMYLACRIS,** Handlirsch.

1906. *Orthomylacris*, Handlirsch, Proc. U.S. Nat. Mus., vol. xxix, p. 768.

Generic Characters.—Tegmina two to two-and-a-half times as long as wide, with a sub-cordate outline. Costal area extending from one-half to two-thirds the length of the tegmen. Radius extending to the tegmen-apex, and giving off a large number of outward branches. Median with few veins, directed towards the apex and the inner margin. Cubitus never reaching the apical margin, and with few branches. Anal area at least twice as long as high. Structure leathery, and with cross-wrinkles.

Orthomylacris lanceolata, Bolton. Plate IX, fig. 5; Text-figure 43.

1911. *Orthomylacris lanceolata*, Bolton, Quart. Journ. Geol. Soc., vol. lxvii, p. 167, pl. x, figs. 1, 2.

Type.—Left tegmen; Museum of Practical Geology, Jermyn Street (no. 24511).

Horizon and Locality.—Coal Measures (shales associated with the Graigola Seam, Pennant Series); Clydach Merthyr Colliery, Clydach Valley, Swansea Vale, Glam.

Specific Characters.—Tegmen long, and uniformly tapering to the apex. Upper surface regularly convex. Subcostal area broadly triangular, with oblique branches. Radius much branched. Median unbranched in basal half, with three outer branches. Cubitus divided into two main branches, the outer forking into two equal twigs, and the inner giving off three inward twigs, the first only forking. Outer and inner margins convex.

Description.—The tegmen, which measures 23 mm. long and 10 mm. wide, lies with the dorsal surface uppermost, and is gently rounded along its length, a slight flattening only being visible over the middle of the outer margin. The uniform tapering of the two margins to the apex produces an elongate form of tegmen of an unusual type among Blattoids. The base of the tegmen is lost, and the costal area appears therefore to occupy nearly half the outer margin.

The subcosta is thin, sunk in the tegminal structure, and gives off three forked branches which pass in straight oblique lines to the margin.

The radius is a large vein, with four branches, the first three doubly-forked and the last undivided. The main stem of the radius is convex in the basal part of its length, and concave in the outer half. The branches pass out very obliquely and extend on to the apical margin.

The median divides about the middle of the tegmen, on a level with the third branch of the radius. It gives off three branches, the first forking twice into four equal twigs, the second of the series forking again near the margin. The inner pair of twigs unite in the middle of their length, and separate again further out, so that a lenticular "cell" is produced. The second branch is undivided. The third branch divides into a long outer twig which bends forwards towards the apex, and a smaller and weaker twig which goes straight out to the inner margin. There is, as a result of this separation, a wide part of the inner margin destitute of veins.

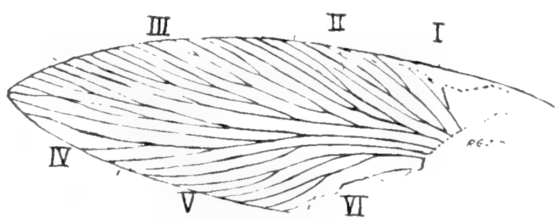

FIG. 43.—*Orthomylacris lanceolata*, Bolton; diagram of venation of left tegmen, three times natural size.—Coal Measures (shales associated with the Graigola Seam, Pennant Series); Clydach Merthyr Colliery, Clydach Valley, Swansea Vale, Glam. Mus. Pract. Geol. (no. 24511). Numbering of veins as in Text-figure 33, p. 104.

The cubitus arises close to the median, and at once divides into two main branches, the outer being forked once only, and the inner giving off a forked branch succeeded by two which are undivided.

The anal area has broken away along the line of the anal furrow. It is shorter than the subcostal area.

The interstitial neuration cannot be determined with certainty. The surface near the apex is marked by cross-wrinkles, but I cannot affirm that this is a part of the neuration.

LARVAL BLATTOIDS.

(Blattoidea) peachi (Woodward). Plate IX, fig. 6.

1887. *Etoblattina peachii*, Woodward, Geol. Mag. [3], vol. iv, p. 433, pl. xii, fig. 1.
1906. *(Blattoidea) peachii*, Handlirsch, Die Fossilen Insekten, p. 178, pl. xviii, fig. 26.

Type.—Upper surface of head, pronotum, rudimentary wings, and broad segmented abdomen, in nodule of fine grey sandstone; Kilmarnock Museum.

Horizon and Locality.—Coal Measures ("grey sandy shale with nodules of impure clay and ironstone" at 91 ft. 6 in. below the surface); Greenhill Pit, Kilmarnock.

Description.—The length of the insect is 23 mm. and its width across the fore-wings 15 mm. The pronotum is 12 mm. wide, and 5 mm. long. The abdomen is 12 mm. long and diminishes in width from before backwards. The coarse character of the stone has obliterated or failed to preserve all the finer detail of the specimen, but the insect still retains the gently convex dorsal surface which it doubtless had during life.

The very small head, not well defined, is apparently divided into two small anterior and two larger posterior areas by shallow longitudinal and transverse grooves. No appendages are visible. A raised V-shaped portion of the matrix in front of the head may indicate that it formerly extended beyond the line of the pronotum. The two anterior plates covering the head are notched in a small V on the middle outer edge.

The pronotum is nearly two-and-a-half times as wide as long, with rounded latero-posterior angles and almost straight posterior border. The front border forms a semicircle, recessed in the middle, and enclosing the head-shield termed by Dr. Henry Woodward an "epicranial plate."

Two pairs of rudimentary wings are present, the first pair articulating well forward, as if attached to the mesonotum under the hinder margin of the pronotum; the hinder pair being joined to the metanotum nearer the middle line. The wings are about 10 mm. long and 5 mm. wide, with blunt apical angles. The front pair of wings have begun to take on the character of tegmina, being stouter than the inner pair.

The venation of the wings is but faintly indicated. Woodward has stated that the "mediastinal" vein and the veins of the anal and intermedian area are seen in all four wings. In present nomenclature this means that the subcosta and the cubitus are present, with some traces of the anal veins.

This seems hardly to be the case. The left hind-wing has the veins best marked, and all that can be said is, that there are indications of a few short, thick veins passing from near the attachment of the wing towards the inner margin, and crossing the middle of the wing. The condition is much like that figured by Comstock and Needham ('Amer. Nat.' [4], vol. xxxii, p. 773, fig. 56, 1898) in the hind-wing of the nymph of a cockroach, except that the veins in the Kilmarnock specimen spread fanwise, instead of keeping in close order down to the wing-apex. The veins present will therefore agree best with the radius, median and cubitus. The vein which I consider the radius is nearly parallel with the outer margin and better defined than the rest.

The length of the mesonotum and metanotum together is 6 mm. Neither is well seen owing to the overlap of the wing-bases.

The abdomen is in excellent preservation, and has several features of interest. It is 12 mm. in length, diminishing from a breadth of 10 mm. across the body and expanded epimera to 3·5 mm. across the ninth segment. The central axis of the abdomen is more convex than the lateral epimera, and the middle line is slightly ridged. The abdomen forms about one-third of the total breadth, being 4 mm. wide in the first segment, diminishing to 1·5 mm. on the ninth segment. The tenth segment is missing.

The epimera are broad, with slightly thickened posterior edges. From the posterior dorsal margins of the first to fourth segments arise thin plate-like expansions. These pass back over the succeeding two segments, showing ragged edges, as if they had a greater extension during life, and had since been partially torn away. The precise relation of these structures to the segments is not quite clear. On the right side of the first, second and third segments, these processes seem to emerge from beneath the hinder edges of the terga. If they do not, but are continuous with the hinder edge, they are yet distinct from the latter, as the suture-line between the adjacent terga can be traced outwards along the front edge of the epimera, and if the two are united this furrow may have functioned as a joint.

The undeveloped wings, scarcely wider than the pronotum, and the broad epimera of the abdomen, clearly indicate the larval condition of the specimen. It must be more advanced towards the adult stage than *Leptoblattina exilis*, Woodw., from the Coal Measures of Coseley, Staffordshire, as it differs considerably in the greater breadth of the abdomen and the development of the epimera.

In size (*Blattoidea*) *peachi* is two-thirds the length of such an adult form as *Aphthoroblattina johnsoni* (Woodw.), and as size is fairly well correlated with development in Blattoids, we may assume that the insect had not fully reached the nymph stage. This conclusion seems to be also confirmed by comparison with the wing-length of *L. exilis*, where the wings are double the length of the pronotum.

The absence of determinable details in the wings prevents any successful attempt to assign the specimen to a position in any accepted classification. The most that can be said is, that the great breadth of the pronotum, as contrasted with the length, would seem to indicate a relationship with the Mylacridæ.

Leptoblattina exilis, Woodward. Plate IX, figs. 7, 8.

1887. *Leptoblattina exilis*, Woodward, Geol. Mag. [3], vol. iv, p. 56, pl. ii, figs. 2, 3.
1906. (*Blattoidea*) *exilis*, Handlirsch, Die Fossilen Insekten, p. 173, pl. xvii, figs. 16, 17.

Type.—Nearly perfect larval blattoid in an ironstone nodule; British Museum, Johnson Collection (no. 1065).

Horizon and Locality.—Middle Coal Measures (binds between the "Brooch" and "Thick" coals); Coseley, Staffs.

Description.—The type-specimen and a second (no. 1066), described at the same time, show an almost complete pronotum, two pairs of rudimentary wings, and a long jointed abdomen. Dr. Henry Woodward recognises a portion of the head projecting in front of the pronotum in each, but of this I am doubtful. He also describes the head as follows: "The head is very small, and somewhat bluntly pyramidal in form, and measures 2 mm. in breadth at its base, where it disappears beneath the pronotum, and is 2 mm. in length. There is a suture visible down the centre which divides the two epicranial plates, at the sides of which the eyes would be seen; in front of the epicranium a small projection no doubt represents the clypeus with the labrum at its extremity."

In the type-specimen (Pl. IX, fig. 7) the pronotum, 7·5 mm. long and 9 mm. wide, is well rounded in front and on the sides, the margin of the latter passing by blunt rounded angles into an almost straight hinder border. The surface is marked out into the usual central raised area, bordered by slight grooves which deepen backwards, and curve inwards. The lateral portions are flattened.

The dorsal part of the mesonotum is partially exposed, its anterior edge being hidden beneath the pronotum. The front pair of wings is attached to the mesonotum so far forward as to touch the hinder edge of the pronotum. The surface of the mesonotum was originally rounded, and judging from its present condition, somewhat thin. It is now slightly puckered by folding.

The metanotum is similar in character to the mesonotum, but a little more robust, and has the second pair of wings still articulated near the front margin.

The abdomen is long, the segments immediately following the body being flattened by pressure, and their boundaries not clearly discernible. Behind follow at least five well-marked segments which decrease in diameter backwards. The last three show lateral epimera with the points turned backwards. Traces of what appear to be cerci follow the last segment. These seem to be curved inwards at their tips, and widely spaced, but their definition is unsatisfactory. The length of the abdomen behind the metanotum is 14 mm., and the last segment is not more than 2 mm. wide, the first of the six segments being double that diameter.

The wings are short, stout structures, those of the right side being perfect, and those of the left side incomplete. The right tegmen has a length of 11 mm., and the hind-wing a length of 10 mm. The venation, as in all larval wings, is very obscure, and can be best studied on the impression of the wings. It consists of a stout vein passing from the point of articulation of the wing outwards towards the wing-apex, and keeping close and parallel with the outer margin. From this vein a series of fine branches spreads fan-wise towards the inner margin of the wing, and seems to reach it. Woodward has recognised a mediastinal (subcostal) vein and an anal vein. An examination of a good cast of the specimen by oblique light shows that there are a strong outer vein parallel with the outer margin, and at least two others with short, thick stems breaking up into a fan-like series of oblique veins which spread out towards the inner margin. From the researches of Messrs. Comstock and Needham (1899, ' American Naturalist ' [4], vol. xxxiii, pp. 573–582, fig. 74), these veins seem recognisable as the radius, median and anal. I am unable to distinguish any detached limb such as that mentioned by Woodward.

The second example (Pl. IX, fig. 8) differs from the first in several small details. It lies on an inclined surface, and the abdomen has been dislocated and twisted over to the right, so that it is in a different plane from the rest of the insect.

The small "head" described by Woodward can be seen projecting from the middle of the frontal margin of the pronotum, which is a little broken away. It consists of a wedge-shaped structure, which narrows forwards, broad at its base and slightly swollen. It is divided into an anterior centrally placed plate of quadrangular outline, the hinder angle joining a sunken line (suture?) dividing the two basal plates, which Woodward terms "epicranial." Too little is seen of the anterior central plate for description, or for its recognition as a labrum.

The pronotum is raised in the centre and hollowed on the sides, while the hinder margin is partially broken away. It overhangs the bases of the first pair of wings. A ridge runs down the median line of the pronotum, the sides of the latter being less rotund than in the first specimen, and the whole pronotum is more sub-pyramidal in form.

The first pair of wings is still in place, and about 11 mm. in length, allowing for the basal part hidden under the hinder margin of the pronotum. The wings stand out at a low angle from the body, leaving the mesonotum and metanotum exposed. Both are partially crushed and crumpled, and the characters cannot be made out. The left wing is the better marked of the two.

The outer margin of the wing of the first pair is stout, and raised above the general level. Two stout ridges rise from the middle of the base and pass along the wing, the second ridge being the strongest, and traceable over two-thirds of the length, while the first ridge does not extend beyond the basal fourth. The first ridge occupies the place of the subcostal vein, and dies out in the direction of the outer margin, but with no evident branches. The second and larger ridge has all the appearance of a radius, is parallel with the outer margin, and can be seen to send off four branches to the middle of the wing-apex, and the inner half of it. The anal area is more slightly ridged, but with no discernible divisions.

The hind-wings have a straighter outer margin than the fore-wings, and are more membranous. Very little is seen of the left hind-wing. The outer margin of the right hind-wing seems to be folded back on itself, and the radius vein is the first distinguishable. It is more branched than its fellow of the fore-wing, giving off at least five branches, the fourth being forked. These branches reach a portion of the outer side, and apex of the wing, and the whole of the inner side of the apical margin. More inward is seen the distal half of another vein which may be the median. It separates into two branches which reach the distal part of the inner margin. The anal area is hidden by being folded in against the body.

The wings appear too small and of too rigid a type to have been serviceable for flight, and the elongated abdomen could not have been supported by such rudimentary wings. The size and condition of the hind-wings shows that the great increase in width over that of the tegmina in the adult form is a comparatively late development, and probably synchronised with the shortening up of the abdomen.

The proximal segments of the abdomen are obscure, but beyond the dislocation can be seen four well-rounded segments, followed by the crushed terminal segment and indications of one of the cerci.

Affinities.—The generic name attached to these specimens by Dr. Woodward is of doubtful value, since in the present state of our knowledge it is impossible to assign larvæ to the adult forms of which they are the immature representatives. The only adult forms known from the same beds are *Archimylacris johnsoni*, *A. eggintoni* and *A. incisa*.

Order PROTODONATA (Brongniart), Handlirsch.

1906. Handlirsch, Die Fossilen Insekten, p. 304.

Large insects with slender bodies similar to those of the Odonata. Wings large, outspread in the condition of rest, and only capable of an up and down movement in one place. Wing-neuration specialised by the union of several longitudinal veins into accessory or interpolated sectors. Cross-nervures well developed in a regular order. Head large, with large eyes and powerful jaws; thorax much as in the Odonata. Legs strong and similar. Antennæ short. Abdomen long.

Family Meganeuridæ, Handlirsch.

1906. Handlirsch, Die Fossilen Insekten, p. 306.

Wings Protodonate in character, with a pre-costal marginal area destitute of veins. Costa almost straight; subcosta simple, and uniting with the costa far out· Radius simple, and followed by a series of accessory veins which represent the radial sector, these all curving towards the distal inner margin. Median apparently united to the radius at the base, and dividing about the middle of the wing into two widely divergent branches, between which are developed a numerous series of accessory veins. Cubitus (in the type species) consisting of a single undivided vein on the outer side, and of an inner branch which is much subdivided. Anal vein reaching middle of inner margin, and giving off many strongly recurved branches. Inner margin broadly convex. Interstitial neuration consisting of numerous series of straight cross-nervures. Wings membranous.

This family was formed for a small group of insects of enormous size, discovered at Commentry and described by Brongniart.

Genus **MEGANEURA**, Brongniart.

1885. *Meganeura*, Brongniart, Bull. Soc. Amis Sci. Nat. Rouen [3], ann. xxi, p. 60.

Generic Characters.—Gigantic insects with long narrow fore-wings and broader hind-wings. Precostal area extending to the middle of the outer margin. Costa almost straight, powerful, and joined far out by the subcosta. Radius a single strong vein, followed by a radial sector arising from the radius in the fore-wing, and in the hind-wing from the outer branch of the median. Median united with the radius at the base, having a simple outer branch and a much divided inner branch. Many of the branches of the latter accessory. Cubitus with outer and inner branches dividing at the base of the wing, and curved in an **S**-shape. The inner branch well divided, the outer feebly so. Anal veins numerous, strongly curved to the inner margin.

Genus **BOLTONITES**, Handlirsch.

1919. *Boltonites*, Handlirsch, Revision der Paläozoischen Insekten, p. 61.

Generic Characters.—Pre-costal field very small; cubitus and anal veins much as in *Gilsonia titana*, Meunier. "The bridge clearly preserved." By this I understand that Handlirsch alludes to the transverse vein which I described as an "oblique inward branch of the cubitus joining on to the anal." Cubitus and anal with few branches.

Boltonites radstockensis (Bolton). Plate X, fig. 1; Text-figure 44.

1914. *Meganeura radstockensis*, Bolton, Quart. Journ. Geol. Soc., vol. lxx, p. 119, pls. xviii, xix.
1919. *Boltonites radstockensis*, Handlirsch, Revision der Paläozoischen Insekten, p. 61.

Specific Characters.—Outer wing-margin thickened, coriaceous and tubercular. Outer and inner wing-margins spinulose. Cubital-anal vein present. Areolæ

(? aborted spiracles) in anal area. Length of wing when complete about 190 mm. or seven and a half inches.

Type.—Proximal third of wing, in dark shale with plant-remains; Sedgwick Museum, Cambridge.

Horizon and Locality.—Upper Coal Measures; Tyning Colliery, Radstock, Somersetshire. Precise horizon uncertain.

Description.—The fragment consists of the proximal portion only of a wing, 64 mm. long and 40 mm. in greatest width, and appears to have formed about one-third of the whole. The wing has also been broken along the middle, and a portion lost, due apparently to the shale breaking irregularly, and leaving an uneven surface. The outer and inner parts of the wing-fragment still retain their normal position relatively to each other, but a portion of the inner part of the base is missing.

The outer part of the specimen consists of two veins, the costa and sub-costa. The inner portion shows the cubital and anal veins. The veins missing are therefore the radius and median.

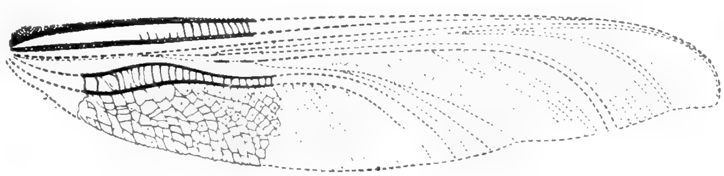

FIG. 44.—*Boltonites radstockensis* (Bolton); restoration of right wing, based on that of *Meganeura monyi*, Brongt., one-half natural size. Upper Coal Measures (precise horizon uncertain); Tyning Colliery, Radstock, Somerset. Sedgwick Museum, Cambridge.

The outer wing-margin consists, not of a free alar expansion, as is usual in the Protodonata, but of a coriaceous and tuberculated mass, which is well marked off from the costa along its whole length. This thickened mass apparently represents the free alar development seen in other members of the group.

That other veins existed in the middle area of the wing is proved by the remains of three short portions of a vein, lying in the middle of the interspace. Not until these fragmentary vein-structures had been perceived, and the type of *Meganeura monyi* studied in the Museum at the Jardin des Plantes, Paris, could its relationship with the Protodonata be confirmed. The direct comparison of the two wings also showed that the Radstock specimen had the same parallelism of the principal veins, the co-existence of similar cross-veins, and the same distinctive character of the anal area as *M. monyi*.

The basal portion of the outer margin of the Radstock wing is swollen into an elongated mass, which thins out distally, and probably did not extend beyond the proximal third of the wing. It can be traced for a length of 20 mm., and near the articulation is covered with numerous low, smooth-topped tubercles, arranged irregularly. The more median part of the costal margin appears as a flat, straight, knife-like edge, crossed by a series of fine striations.

The thickened pre-costal portion of the outer margin forms a rigid bar, enormously strengthening the wing for flight. The costa is distinct, and passes directly to the wing-apex, as a broad, strap-shaped vein, broadest at its point of origin, and slowly diminishing in width to the tip of the wing.

The subcosta has an apparent union at its base with the costa, but this is due to a slight backward displacement of the latter. Some distance beyond the thickened margin, the costa bears, at regular intervals, a series of low spines, projecting freely forwards, and gradually inclining towards the wing-apex. A few scattered tubercles, and a faint ridge, are seen along the middle of the vein, and eventually die out. The distal part of the costa is straight, and is joined to the subcosta by a series of transverse branches which are well marked. Of these branches, eleven are still whole, and portions of nine others can be made out. It would therefore seem that the whole of the costal area was covered by a parallel system of straight cross-branches with no intervening network.

The subcosta arises in close contact with the costa, diverging rapidly until the two are about 5—6 mm. apart. Once this distance has been attained, they remain nearly parallel for some distance. There are indications that the two come together some distance beyond the broken edge of the wing-fragment.

The costa and subcosta are nowhere more than 5—6 mm. apart, in the main but 4 mm., the interval narrowing to the broken edge of the wing. While the subcosta has the same flat, strap-shaped character as the costa, it is more delicate, and a narrower vein. A few tubercles are disposed along the median line of its length.

The radius and median veins being lost, except for the trivial pieces already noted, they cannot be compared with those of *Meganeura*. In the French species of this genus a complex of parallel veins arises from one or two roots between the subcosta and the cubitus. In the case of *M. monyi*, this complex arises from a strong radius and a weak median. In *M. selysii* it would appear that the radius and median are united at their base. In the restoration of the Radstock wing it will be seen that the vein-fragments appear as parts of the median vein, the radius being wholly lost.

The cubitus is separated from the outer part of the wing by the interval formerly occupied by the radius and median. This interval is variable in width, owing to the strong curvature of the cubitus. This is a large flattened vein, strongly flexuous, and finally curving inwards to reach the middle of the inner margin. The base of the vein has been broken away and lost, but its course may be indicated by a faint groove which curves forward towards the base of the subcosta. The outer inward curve of the cubitus is the greater, so that the interval between the radius and the subcosta becomes increasingly wide, thus agreeing exactly with what obtains in the same part of the wing in *Meganeura monyi*. It is an indication of the rapid inward curvature which takes place a little further out, and of the presence in the complete wing of the wide distal area occupied by the many branches of the radius and the median.

Close to the basal broken end of the cubitus a strong oblique inward vein is given off, which reaches the anal vein, and fuses with it. At the time when I first described this wing I wrote as follows: "It has the appearance of an important commissure between the cubitus and the anal, or of a posterior branch of the former which has fused with the latter." Since then, Dr. R. J. Tillyard has published the results of his studies on recent dragon-flies ('The Biology of Dragon-flies,' Cambridge University Press, 1917), in which he notes our discovery of this oblique vein. He recognises it as an anal-cubital vein which he had previously ('Proc. Linn. Soc., N.S.W.,' vol. xxxix, pp. 163—216, 1914) described as indicating the point where the true anal vein diverges from the cubitus. He concludes (*op. cit.*, p. 305): "Hence it would appear that *Cu* (cubitus) and *A* (anal) were fused basally as in all recent forms. Thus the gap between Protodonata and Odonata is being gradually lessened until to-day we may almost certainly see in the Meganeuridæ the giant relatives of the direct ancestors of some at least of our recent families."

Beyond this anal-cubitus vein the cubitus is joined to the anal by a system of parallel slightly curved branches, similar in character to those which unite the sub-costa and the costa. No fewer than twenty-five of these branches can be distinguished. Basally to the anal-cubital vein are two transverse branches, a little more curved than the rest. As in the costa and sub-costa, a median line of tubercular ornament is present.

The anal vein is strongly marked, and its course is much similar to that of the cubitus, but the second inward flexure is less marked, so that the two veins are closer together in the middle of their length, and more widely separated basally. The anal gives origin, along the whole length of its hinder margin, to a series of branches, which arise at slightly increasing intervals, being closest basally, and most widely separated between the twelfth and thirteenth branches, beyond which the interspaces narrow again to the fifteenth branch. The basal branches pass in straight or slightly oblique lines inwards to the wing-margin. Further out they become curved, with the convexity outwards. The twelfth branch is a strong and important vein, sweeping in a powerful double curve distally, and inwardly to the wing-margin. It corresponds in position to Brongniart's "vein X." Beyond it are the remains of three feebler branches, which bend in simple curves to the margin.

The spaces between the anal branches are divided up into a series of quadrangular areas or cellules, by a great series of secondary branches, arising at right-angles. The twelfth dorsal branch stands out from the rest by reason of its robust character and sweeping curve, and gives off, on its inner side, a series of twigs, which divide and separate so widely that first a double and then a treble series of cellules are enclosed between them. On its distal side it intercepts five branches arising from the inner border of the main stem of the anal, the enclosed quadrangular areas being increasingly elongated antero-posteriorly up to the eighteenth branch, the course of that branch to the margin being uninterrupted. The integument in many of the quadrangular areas or cellules is marked by a slight central elevation, which, under high magnification, presents the appearance of a circular thickened lip, with a central depression or perforation. These structures have no regularity of arrangement, but are most numerous on each side of the twelfth branch of the anal. The integument within the cellules is, in some instances, obliquely wrinkled. These structures appear to resemble aborted spiracles.

The inner margin of the wing is sharply sloped forwards from the broken edge onwards to the point of attachment, and is well-defined and spinous along the whole or the greater part of its length. The spines are low, directed distally, and in character somewhat like those on the outer margin of the wing. They are not so clearly shown, however, and they may not be truly marginal, as it is a matter of doubt whether the integument stretches a little outside them. I incline to the latter view. The ventral surface of the wing seems to be uppermost, in which case the wing-fragment is the proximal portion of a right wing.

Affinities.—The general characters of the wing-fragment are those typical of the genus *Meganeura*, and it cannot be confused with the genus *Paralogus*. It is, however, unlike *M. monyi*, in which the development of marginal spines has not been recorded, and the tuberculation so characteristic of the Radstock wing is not shown in that species. *M. monyi* is a wider and longer wing, and does not possess the areolæ seen in the quadrangular cellules of this species.

Considered as a Meganeurid wing, the Radstock specimen is no primitive structure, but highly specialised, an anal cubitus connection is present, the costal border has become thickened and tuberculated, and a secondary development of spinules and tuberculations has arisen.

INCERTÆ SEDIS.

Genus **TILLYARDIA**, novum.

Generic Characters.—Wings elongated, five times as long as wide. Subcosta short; radius simple, radial sector forming an accessory vein with several divisions. Median vein with few branches. Cubitus with two main branches, the inner much divided. Accessory sectors present. Interstitial neuration forming a regular series of straight cross-nervures.

I refer to this genus a highly specialised wing from the Scottish Coal Measures, which is unlike any other Carboniferous wing that I know. It is at once suggestive of the Palæodictyoptera and of the Protodonata, but belongs, I believe, to the latter Order. Where shown, the neuration of the wing is clear, and the absence of the outer part of the base, and the central portion of the wing, renders it difficult to determine the actual course of certain veins and their true nature.

I have much pleasure in naming this genus after Dr. R. J. Tillyard, whose researches on the venation of the wings of nymphs of recent insects have helped to interpret the older fossil forms.

Tillyardia multiplicata, sp. nov. Plate X, fig. 2; Text-figure 45.

Type.—Greater part of the impression of the under surface of a right wing; Museum of Geological Survey of Scotland, Edinburgh (no. T. 4098*b*).

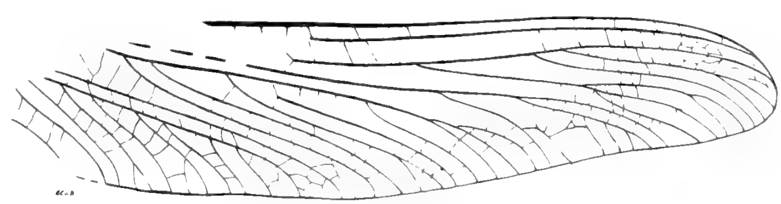

FIG. 45.—*Tillyardia multiplicata*, sp. nov.; diagram of venation of right wing, enlarged one-and-a-half times. Upper Coal Measures; Barony Pit, Auchinleck, Ayrshire. Museum of Geological Survey of Scotland, Edinburgh (no. T. 4098 *b*).

Horizon and Locality.—Upper Coal Measures; Barony Pit, Auchinleck, Ayrshire.

Specific Characters.—As above.

Description.—The wing lies on the irregular surface of a soft purple sandstone, is imperfect, and has been badly rubbed, so that the junctions of some of the veins have been obscured. The whole of the base of the wing is missing, and the middle portion of the impression of the wing has also been destroyed. It is 67 mm. long and 13 mm. wide.

The outer margin appears to have been almost straight over the greater part of its length, inclining gently into the wing-apex, the latter joining the inner margin in a blunt right-angle. By analogy with the Protodonata, the outer margin was extended outwardly in its basal half, and the subcostal area was widened out. This feature is seen in *Paralogus æschnoides*, Scd., with which the wing has much in common. No trace of an undoubted subcostal vein is distinguishable. It must therefore have been short, and joined to the outer margin in the basal half. The radius is a long vein, parallel with the outer margin, and reaching the wing-apex, curving inwards as it does so. The junctions of the branches of the radial sector are destroyed. It would seem to have begun between the radius and the median as an accessory vein, rather than as an offshoot of the radius. Its branches occupy the outer half of the wing-apex. The median is a large and important vein, dividing near the base into two branches. The outer branch is undivided until close to the distal end of the outer margin, where it gives off an outer and two inner twigs. The inner branch of the median gives off five simple inner twigs, and an outer one which forks close to the margin. The cubitus is represented by two veins, an outer vein which remains undivided and an inner which gives off at least five twigs. It is possible that the vein which I thus describe as the cubitus is really part of a cubito-anal, but as the basal part is missing the exact conditions cannot be determined. The inner margin of the wing is nearly straight.

Affinities.—The wing-structure, so far as it can be made out, is much like that of *Paralogus æschnoides*, Scd., and *Protagrion audouini*, Brong., and of these it more nearly accords with the latter in its great length as contrasted with the breadth. The plication of the wing is unusually well developed, and is a feature best seen in *P. æschnoides*. The presence of accessory sectors is again a feature seen in *Protagrion*. The general wing-structure, therefore, has certain characters of both genera, and where it departs from the one it approaches the other.

ADDENDUM.

Archimylacris pringlei, Bolton. Plate X, fig. 3.

1921. *Archimylacris pringlei*, Bolton, Quart. Journ. Geol. Soc., vol. lxxvii, pp. 23—29, pl. i, figs. 1—2, text-fig. 1.

Type.—The basal two-thirds of a fore-wing, and counterpart impression, partly obscured by plant remains; Museum of Practical Geology, Jermyn Street (nos. 30725, 30726).

Horizon and Locality.—Keele Group, Upper Division of the Coal Measures; from rocks between the surface level and 97 feet in borehole at Slang Lane, Wellington, Shropshire.

Specific Characters.—Wing twice to two-and-a-half times as long as wide, costal margin flattened; subcostal area strap-shaped and very wide, crossed by numerous parallel branches of the subcosta. Radius dividing beyond middle of wing. Median parallel with radius. Cubitus curving to inner margin, with widely separated inward branches. Anal area long.

Description.—The wing-fragment has a length of 18 mm. The costal margin is flatly convex over the greater part of its length, and well rounded at the base of the wing. The subcosta is parallel to and widely spaced from the outer margin, to which it sends eight or nine branches, two of which are forked, and one, the most distal, is not fully developed. The radius is not complete, and has but a slight divergence from the subcosta. It gives off the radial sector at a point between the seventh and eighth branches of the subcosta. The radial sector goes out to the wing-apex, sending its branches forward to the outer margin. The median diverges a little more from the radius than the latter from the subcosta. Portions of three inner branches are present. The cubitus is a convex vein passing well out to the distal end of the inner margin of the wing, and giving off a series of widely separated inward branches, of which four are present on the wing-fragment preserved. Owing to the forward displacement of the anal portion of the wing, the first branch of the cubitus passes under the first anal vein. The second shows a simple fork, and the remaining two veins end undivided on the line of fracture. Portions of six anal veins are present, the first obscure and the rest parallel. The interstitial neuration consists of a compact series of close-set transverse nervures, which in the basal areas between the radius, median, and cubitus unite laterally and irregularly until they form a coarse irregular meshwork.

Affinities.—The widely spaced subcosta and the character of the interstitial neuration of the wing show a close relationship to that of two forms of *Archimylacris* (*A. desaillyi* and *A. lerichei*) recorded from the Coal Measures of Liévin, Northern France, but, as the accompanying tabulated comparison will show, the wing is nevertheless specifically distinct from either.

Observations.—The presence of this fossil Blattoid in the Keele Group of the Upper Division of the Coal Measures of Shropshire, and its specific relation to forms known only from the Westphalian Series of Liévin, Northern France, is a matter of considerable interest, especially as Dr. Pruvost, of Lille, had previously drawn attention to the fact that the fauna at the top of the Coal Measures in Great Britain (Keele Group, Newcastle-under-Lyme Group, Etruria Group) does not notably differ from the fauna at the top of the Westphalian in Northern France.

TABULATED COMPARISON.

A. pringlei, Bolton.	*A. desaillyi*, Leriche.	*A. lerichei*, Pruvost.
Costal Area:		
Strap-shaped, widely spaced from wing-margin.	Strap-shaped, widely spaced from wing-margin.	Outer third oblique to wing-margin.
Subcostal Vein:		
Numerous divisions, mostly forking.	Numerous divisions, mostly forking.	Few divisions, much branched.

	A. pringlei, Bolton.	*A. desaillyi*, Leriche.	*A. lerichei*, Pruvost.
Radius Vein:	Few branches. Radial sector arising opposite outer fourth of subcosta.	Seven branches. Radial sector arising opposite outer third of subcosta.	Twelve branches. Radial sector arising opposite middle of subcosta.
Radial Sector:	Branching not known.	Eight branches.	Seven to eight branches.
Median Vein:	Branches beyond origin of radial sector.	Branches opposite first fork of radial sector.	Branches much beyond origin of radial sector.
Cubitus Vein:	First branch simple, second forked.	First branch simple, second and third forked.	First branch dividing into four, second simple, third and fourth branched.
Anal Veins:	Undivided.	First vein only forked.	First anal forking twice.
Interstitial neuration:	Transverse nervures, except in the median basal part of the wing, where it is reticulate.	Transverse nervures, except in the median basal part of the wing, where it is reticulate.	Transverse nervures, except in the median basal part of the wing, where it is reticulate.

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NOTE.—The roman and arabic numerals following a semicolon refer to the plates and figures illustrating those species which are recognised and described.

PLATE V.

FIG. PAGE.

1. *Geroneura (?) ovata*, sp. nov.; impression of upper surface of apex of left wing. × $1\frac{1}{2}$. Middle Coal Measures (binds between "Brooch" and "Thick" Coals); British Museum (Madeley Coll.), no. I. 2965. 77.

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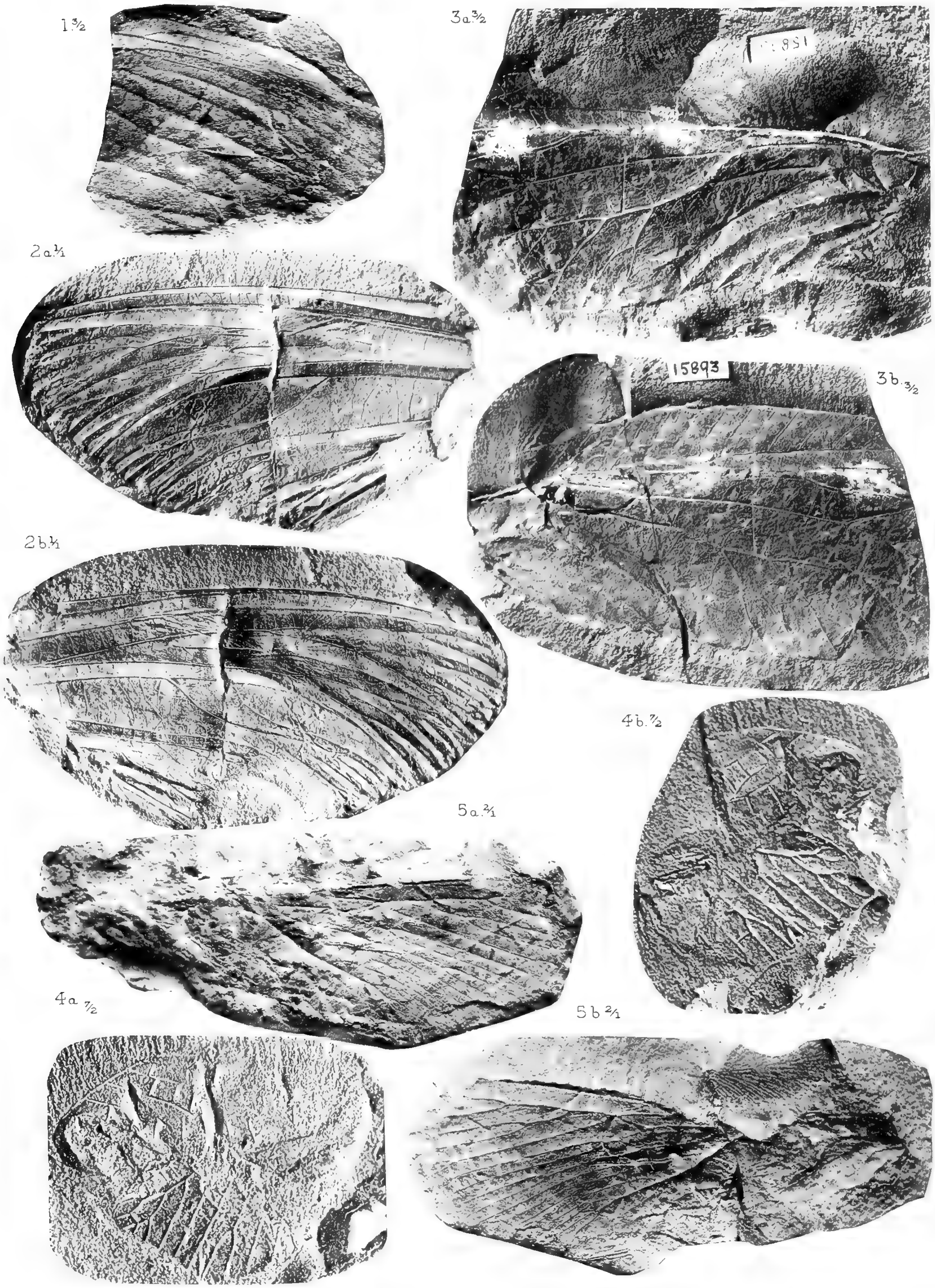
5 *b*. Ditto; impression of same. × 2. 85.



1. GERONEURA? 2. ÆDŒOPHASMA. 3. COSELIA.

4. GENENTOMUM. 5. XEROPTERA.

J W Tutcher, photo

PLATE VII.

Fig.		Page.
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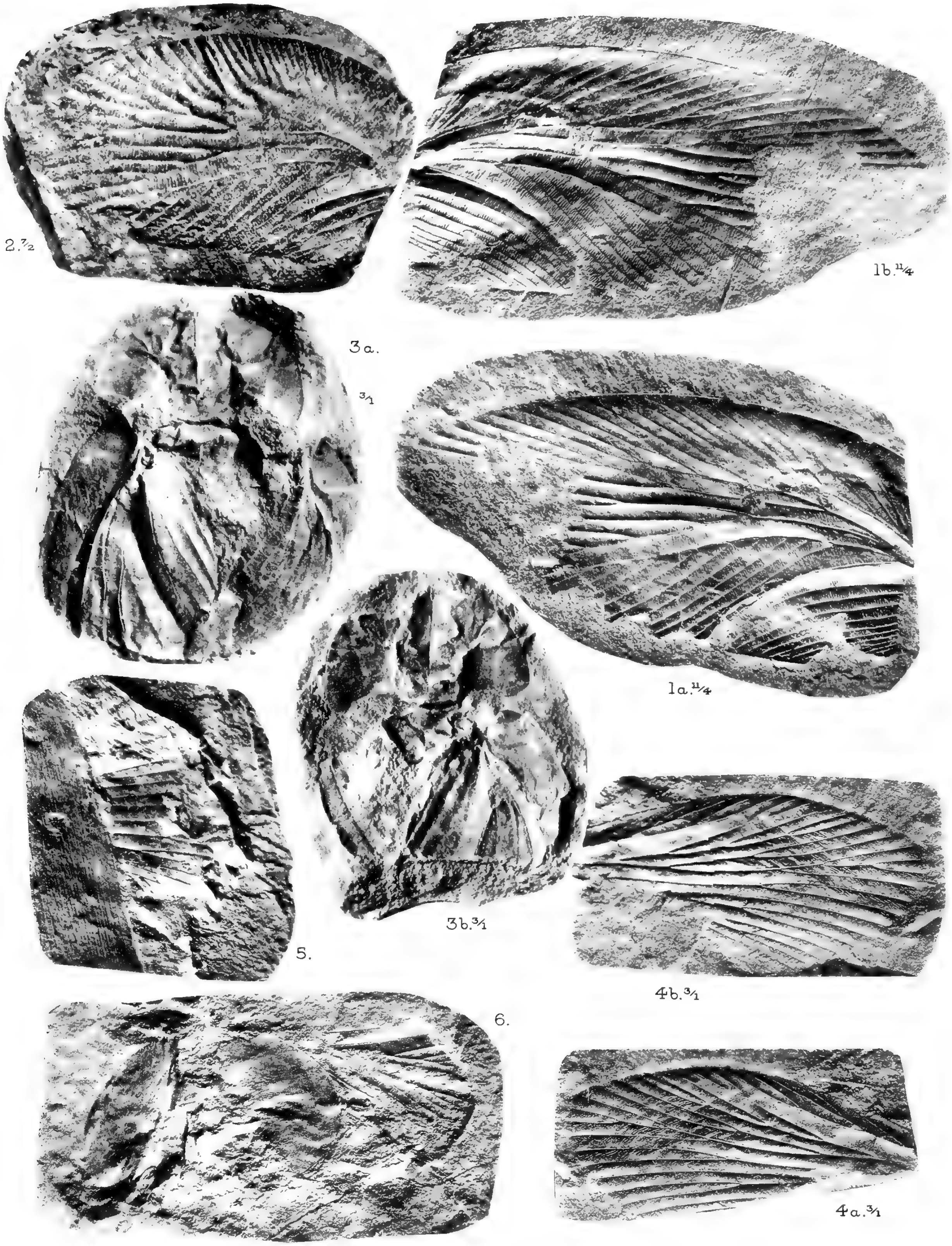

1-6. ARCHIMYLACRIS.

J. W. Tutcher, photo. London Stereoscopic Co. imp.

PLATE VIII.

Fig.		Page.
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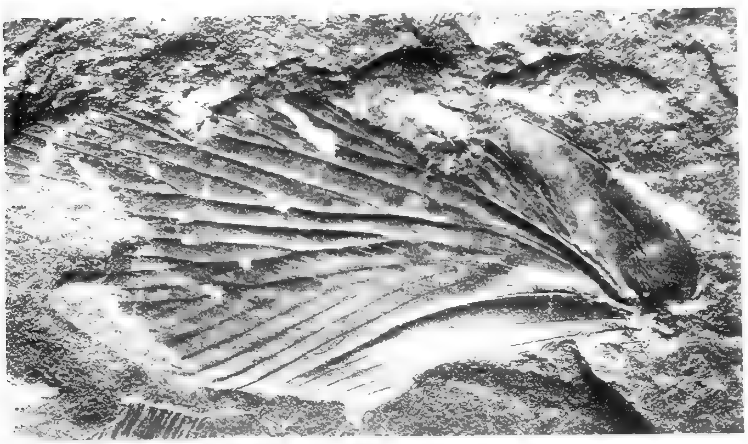
Bolton. Insects of Coal Measures.

PLATE VIII.

1b. 3/1

2. 1/1



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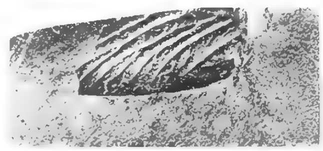

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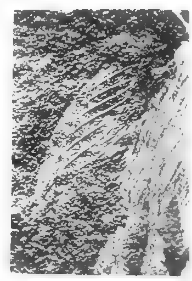
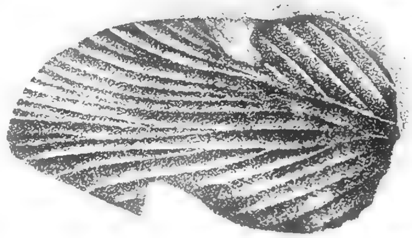


4b. 9/2

7. 5/2



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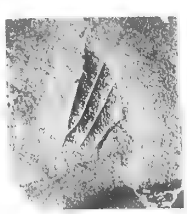
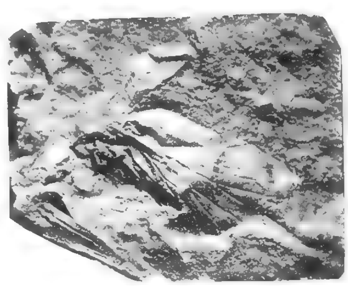


5a. 9/2

5b. 9/2



8. 7/2

1. 2. 4. 5. PHYLOBLATTA. 3. ARCHIMYLACRIDAE.

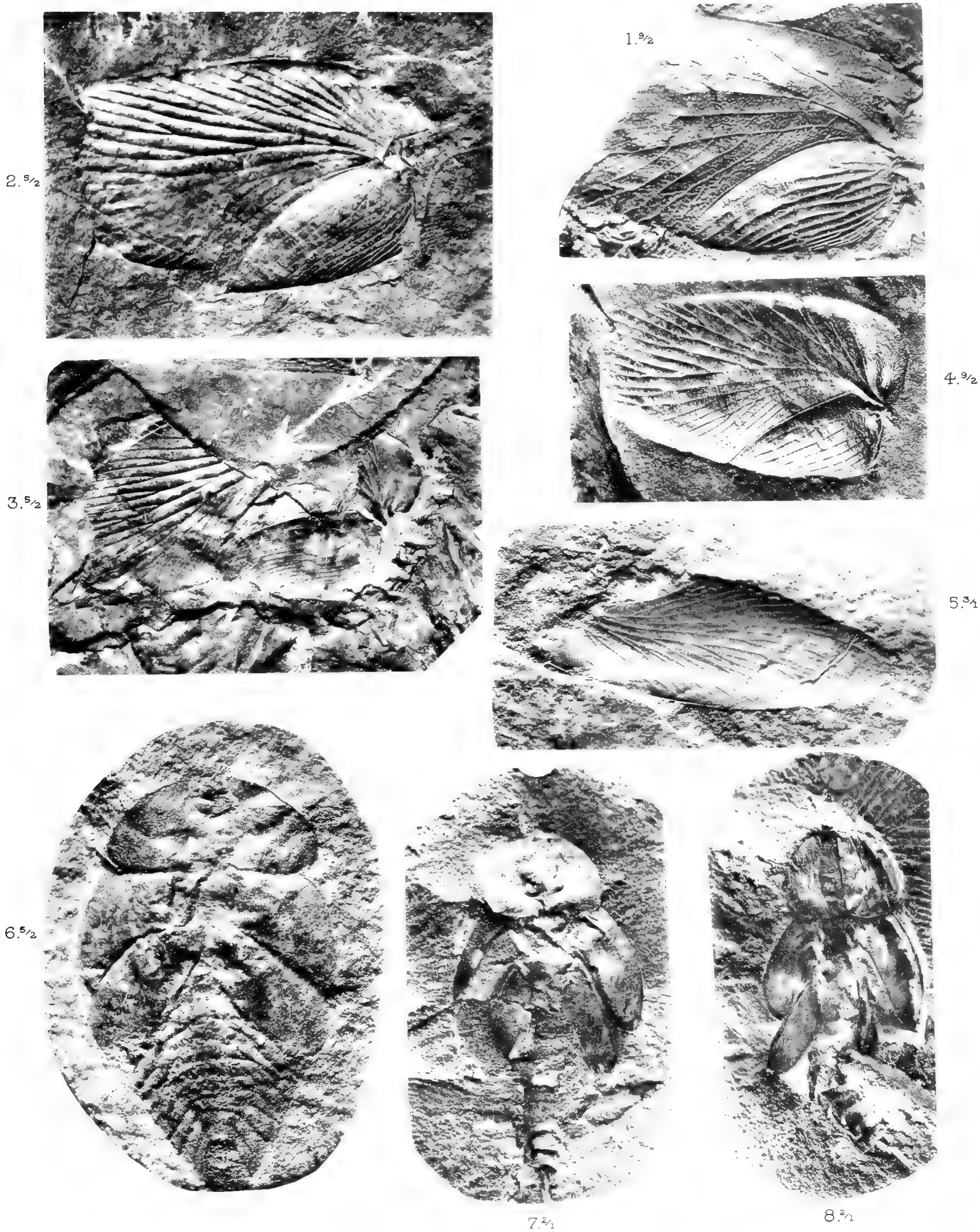
6. BLATTOID WING FRAGMENT. 7. 8. HEMIMYLACRIS.

J. W. Tutcher, photo

London Stereoscopic Co. imp.

PLATE IX.

Bolton. Insects of Coal Measures. PLATE IX.



1. PHYLOMYLACRIS. 2-4. SOOMYLACRIS. 5. ORTHOMYLACRIS.
6. (BLATTOIDEA.) 7. 8. LEPTOBLATTINA.

J. W. Tutcher, photo. London, Stereoscopic Co. imp.

PLATE X.

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1*c*.	Ditto; distal portion of the costa and subcosta, showing the spinous anterior border of the former, the cross-branches uniting the two veins, and a median line of tubercular ornament on the subcosta. × 4.	140.
1*d*.	Ditto; proximal portion of the inner margin, showing the development of stout submarginal spines. × 4.	140.
1*e*.	Ditto; more distal portion of the inner margin, showing the submarginal spines. × 4.	140.
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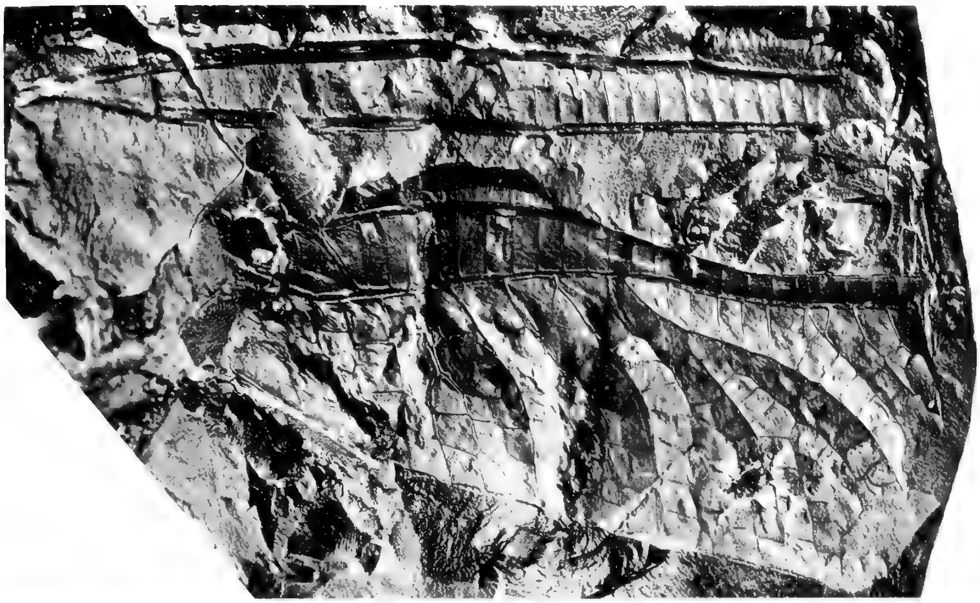
2.

3/2



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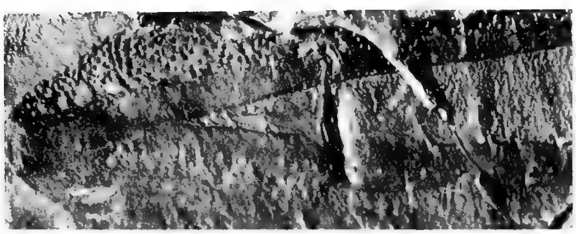

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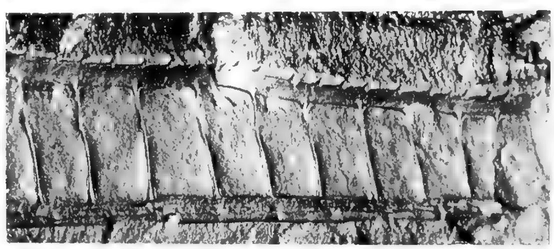

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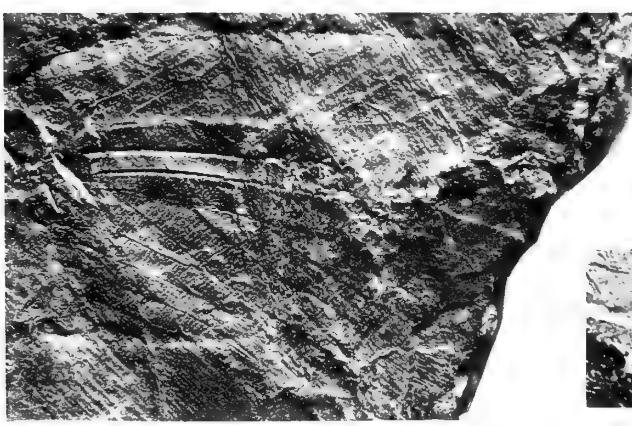

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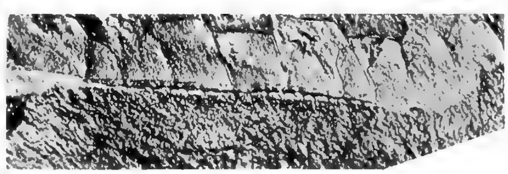

1e.

4/1

1d.

4/1

1a-e. BOLTONITES. 2. TILLYARDIA.

3. ARCHIMYLACRIS.

J. W. Tutcher, photo London Stereoscopic Co. imp

Palæontographical Society, 1920.

A MONOGRAPH

ON THE

BRITISH PLEISTOCENE MAMMALIA

VOL. III, PART I.

HIPPOPOTAMUS.

BY

SIDNEY H. REYNOLDS, M.A., Sc.D., F.G.S.,
PROFESSOR OF GEOLOGY IN THE UNIVERSITY OF BRISTOL.

Pages 1—38; Plates I—VI.

LONDON:
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July, 1922.

inhabitant of north-western Europe manifested itself even earlier in England than on the Continent, an old tract published in 1669 recording the finding at Chartham near Canterbury of bones and teeth which were regarded as hippopotamine. Owen, however, states that the accompanying figures of the teeth were quite good enough to show that the animal in question was a rhinoceros.

The occurrence of the hippopotamus in England was clearly established by a number of observers early in the nineteenth century. Parkinson[1] (1811) accurately described teeth from Walton, Essex, these being now preserved in the Royal College of Surgeons' Museum. Trimmer[2] (1813) gave an excellent account of bones found in river gravel near Brentford, and Strickland[3] (1834) of others found in the Avon valley near Worcester.

The earliest record of the hippopotamus from a British cave is contained in Buckland's classical account of the Kirkdale cave (1822).[4] The teeth found were mainly milk-molars and permanent molars which had not yet cut the jaw, from which the inference was drawn that it was young and inexperienced individuals that fell victims to the Kirkdale hyænas.

Meanwhile, the wonderful series of hippopotamine remains from the Val d'Arno was attracting more attention, and was briefly described by Breislak[5] (1822). Cuvier had had an opportunity earlier than this of examining some of the bones, and it was on them that he based his view that the fossil form *Hippopotamus major* was distinct from the living species, and indeed differed from it as much as the fossil species of rhinoceros and elephant differed from their living congeners. Nesti[6] (1820) gave a full account with three plates of the Val d'Arno hippopotamus. He followed Cuvier in considering the fossil form to be a distinct species, as did Pictet[7] in his 'Paléontologie' (1844) and Owen[8] in his 'History of British Fossil Mammals and Birds' (1846), in which, in addition to various Pleistocene specimens being described, a fine mandible from the Forest Bed of Cromer is figured.

Even more remarkable than those of the Val d'Arno were the masses of bones of hippopotamus found in the caves of San Ciro and Maccagnone near Palermo, Sicily, and described by Falconer[9] (1860).

The splendidly illustrated section of de Blainville's 'Ostéographie' dealing with the hippopotamus was published in 1844, and the historical account of the discovery of hippopotamine remains which it contains has already been alluded to. De Blainville discusses the evidence on which Cuvier based his view that the fossil

[1] 'Organic Remains,' iii, p. 375.
[2] 'Phil. Trans.,' ciii, p. 131.
[3] 'Proc. Geol. Soc.,' ii, p. 111.
[4] 'Phil. Trans.,' cxii, p. 182.
[5] 'Traité sur la structure extérieure du Globe,' ii, p. 352.
[6] 'Mem. Soc. Ital. Sci.' (Modena), xviii, p. 415.
[7] I., p. 252.
[8] P. 399.
[9] 'Quart. Journ. Geol. Soc.,' xvi, p. 99. For an account of this deposit and a suggestion as to how it may have accumulated see W. B. Wright, 'The Quaternary Ice Age' (1914), p. 248.

Hippopotamus major was distinct from the living *Hippopotamus amphibius* and concludes that there is no specific difference between the two forms.

Most of the British hippopotamine remains known as yet were from the Thames valley, but in 1853 Denny[1] described a remarkably fine series of bones from Wortley near Leeds. The bones were associated and unworn, suggesting that the animal lived on the spot. Denny also alluded to the occurrence of the hippopotamus at Overton near York, and this still remains the most northerly record of its occurrence. Next to the series from Barrington, to be alluded to later, the Leeds series is still the most nearly perfect from Britain.

Some of the remarkable small hippopotami from islands in the Mediterranean were early described, *H. pentlandi* from Sicily by H. von Meyer[2] in 1832, *H. minutus* from Malta, first described by Cuvier, more fully by de Blainville[3] in 1847.

In 1836 appeared Falconer and Cautley's[4] first account of the fossil hippopotami of the Siwalik Hills, followed in 1847 by the 'Fauna Antiqua Sivalensis,' in which ten fine plates were given of hippopotamine remains, and the generic names *Tetraprotodon* and *Hexaprotodon*, based on the number of the incisor teeth, were proposed. These forms are described in Falconer's 'Palæontological Memoirs' (1868).

In 1860 Falconer[5] published (in abstract) his first paper on the Gower caves, in which he records *Hippopotamus* from Ravenscliff cave. Other cave records of hippopotamus are by an anonymous writer[6] (1843) from Durdham Down, Bristol, and by Falconer (1868) from Cefn, near St. Asaph.[7] At Ravenscliff, as at Kirkdale, the teeth include those of very young individuals.

In 1866 Boyd Dawkins, in the Introduction to the first of the Palæontographical Society's monographs on the British Pleistocene Mammalia, by himself and W. A. Sanford, gave a valuable summary of the occurrence and association of the Pleistocene hippopotamus. In this introduction and in two papers—"On the Pleistocene Climate and on the Relations of the Pleistocene Mammalia to the Glacial Period"[8] (1871), and the "Classification of the Pleistocene Strata of England and the Continent by Means of the Mammalia"[9] (1872)—one of the subjects considered is

[1] 'Proc. Geol. Polyt. Soc. Yorksh.,' iii, p. 321.

Note.—The skull from a Lancashire peat bog noticed by C. Leigh ('Nat. Hist. Lancashire,' 1700, p. 185), though accepted as fossil by Buckland and by Owen, is doubtless correctly regarded by Woodward and Sherborn as a buried recent specimen.

[2] 'Palæologica,' p. 533.

[3] 'Ostéographie,' vii, p. 65.

[4] 'Asiatic Researches,' xix, p. 40.

[5] 'Quart. Journ. Geol. Soc.,' xvi, p. 487.

[6] 'Geologist,' ii. p. 71. A further account is given by E. Wilson, 'Proc. Bristol Nat. Soc.,' N.S., v (1885), p. 31.

[7] 'Palæont. Mem.,' ii, p. 581.

[8] 'Pop. Science Review,' x, p. 388.

[9] 'Quart. Journ. Geol. Soc.,' xxviii, p. 410.

the occurrence of the hippopotamus as far north as York and the association of its bones with those of boreal animals like the mammoth. The subject, which was fully discussed at about the same date by J. Geikie[1] (1872), had already been considered by Lyell and Prestwich. The various explanations suggested are discussed in the sequel (p. 7).

At this date Boyd Dawkins was of the opinion that the Pleistocene form *H. major* was distinct from *H. amphibius.* The same opinion was held by Falconer. Other records from various parts of England now followed—by Thompson[2] (1869) from Motcomb, Dorset; by Busk[3] (1872) from the Thames Valley at Acton and Turnham Green; by Boyd Dawkins and Mello[4] (1879) from Cresswell Crags. In his paper on the distribution of British post-glacial mammals[5] (1869) Boyd Dawkins mentions twenty-four localities where *Hippopotamus* had been found in river deposits and four in caves.

In 1884 appeared Lydekker's important memoir on the Bunodont Suina of the Indian Siwalik and Narbada beds.[6] He suggested the merging of Falconer and Cautley's genera *Tetraprotodon* and *Hexaprotodon*, and even of Leidy's genus *Chœropsis*, in the genus *Hippopotamus.* In opposition to the ordinary view he considered the missing incisor in *H. amphibius* to be the second, not the third. In his 'Catalogue of the Fossil Mammalia in the British Museum' (1885) Lydekker included all the Hippopotamidæ in the genus *Hippopotamus.*

Although de Blainville as early as 1844 had affirmed[7] the identity of the fossil *H. major* with the living *H. amphibius*, nearly all subsequent writers had continued to regard the two as distinct species. This was the case, for example, with Forsyth Major[8] in his paper on the Mammalian fauna of the Val d'Arno (1885). Boyd Dawkins, however, in a note appended to this paper, stated his belief that the two belong to the same species, and Lydekker expressed his agreement with him. Later writers, including Woodward and Sherborn[9] (1890) and Boule[10] (1910) have accepted this conclusion.

Next to those of the Val d'Arno and Palermo, probably the most remarkable accumulation of hippopotamine bones found in Europe, is that of Barrington near Cambridge,[11] where the remains of a whole herd, including individuals of all ages, were discovered in 1878. Osmond Fisher[12] (1879) first gave an account of the deposit,

[1] 'Geol. Mag.,' ix, p. 164.
[2] *Loc. cit.*, vi, p. 206.
[3] 'Quart. Journ. Geol. Soc.,' xxviii, p. 465.
[4] *Loc. cit.*, xxxv, p. 724.
[5] *Loc. cit.*, xxv, p. 192.
[6] 'Palæont. Indica,' ser. 10, iii, p. 35.
[7] 'Ostéographie,' fasc. vii, p. 61.
[8] 'Quart. Journ. Geol. Soc.,' xli, p. 1.
[9] 'Catalogue of British Fossil Vertebrata,' p. 351.
[10] 'Les Grottes de Grimaldi,' i, fasc. iii, p. 193.
[11] For an illustrated account of the Barrington Beds see Hughes, 'Proc. Geol. Assoc.,' xxii (1911), p. 268. See also Boule, 'Bull. Soc. Géol. France' [4], vii (1907), p. 382.
[12] 'Quart. Journ. Geol. Soc.,' xxxv, p. 670.

and in 1885 Lake[1] described a peculiar mandible which he considered to be that of a female—an opinion in which he was supported by Lydekker.

During the past thirty years no papers of a general character bearing on the Hippopotamidæ have been published in English, but the occurrence of the hippopotamus has been recorded from a number of additional British localities, *e.g.* by Bemrose and Deeley[2] (1896), from Derby; by Hinton[3] (1889), from Ilford; by Dawson and Woodward[4] (1913), from Piltdown.

Several supposed new species were described by Pomel[5] from Algiers in 1896. Stehlin[6] (1899, and again in 1908) has briefly discussed the possible origin of the Hippopotamidæ.

II. DISTRIBUTION OF THE HIPPOPOTAMUS IN BRITAIN.

It was apparently not till the very end of the Pliocene period that the hippopotamus reached Britain, the earliest British remains being those from the Norfolk Forest Bed of Bacton, Happisburgh and Cromer. These remains, which are mainly isolated teeth but include one very fine mandibular ramus, were first recorded by S. Woodward[7] in 1833, and were described by Owen[8] (1846) and afterwards alluded to by Newton[9] (1882).

During Pleistocene times the hippopotamus was very widely distributed in England, ranging as far west as Torquay and Plymouth and as far north as Overton, Yorkshire. The majority of the records are, however, from the Thames valley and eastern counties of England. That the hippopotamus extended into Wales is shown by the occurrence of teeth in the caves of Ravenscliff, Gower,[10] and Caldy Island in South Wales, and of Cefn[11] near St. Asaph in North Wales. No suggestion has ever been made that the hippopotamus reached Scotland, and though a tooth is stated to have been found in Antrim it is probable that this was a mistaken record.[12]

[1] 'Geol. Mag.' [3], ii, p. 318.
[2] 'Quart. Journ. Geol. Soc.,' lii, p. 497.
[3] 'Proc. Geol. Assoc.,' xvi, p. 277.
[4] 'Quart. Journ. Geol. Soc.,' lxix, p. 142.
[5] 'Carte Géologique d'Algérie, Paléont. Monog.'; according to Boule ('Grottes de Grimaldi,' i, fasc. iii, p. 195) these are varieties of *H. amphibius*.
[6] 'Abhandl. Schweiz. Palæont. Ges.,' xxvi (1899), p. 433, and xxxv (1908), p. 751.
[7] 'Geol. of Norfolk,' p. 46.
[8] 'Brit. Foss. Mammals,' p. 399.
[9] 'Vertebrata of Forest Bed Series of Norfolk and Suffolk' (Mem. Geol. Surv.), p. 42.
[10] 'Quart. Journ. Geol. Soc.,' xvi (1860), p. 490
[11] H. Falconer, 'Palæont. Mem.,' i, p 541.
[12] Adams ('Journ. Roy. Geol. Soc. Ireland,' iv, 1877, p. 247) refers to this as follows: "The presence of the hippopotamus in Ireland rests on a canine tooth said to have been discovered in the county of Antrim, a drawing of which tooth is preserved in the office of the Geological Survey of Ireland."

The subjoined list includes fifty-three localities where the hippopotamus has been found in river deposits, and twelve in caves or fissures, as compared with twenty-four of the former and four of the latter in Boyd Dawkins' list[1] of 1869.

TABLE SHOWING THE DISTRIBUTION OF THE HIPPOPOTAMUS IN BRITAIN.

RIVER DEPOSITS.

Acton, Middlesex.
Alconbury, Hunts.
Allerton, Derby.
Barnwell, Cambridge.
Barrington, Cambridge.
Bacton, Norfolk.
Bedford.
Brentford.
Brighton.
Bugbrook, Northants.
Bungay, Suffolk.
Burfield, Berks.
Cambridge Botanical Gardens.
Camden Town.
Chelmsford.
Chedzoy, Somerset.
Cold Higham, Northants.
Coulsdon, Surrey.
Cropthorne, Worcestershire.
Eastbourne.
Eckington on Avon, Worcestershire.
Evesham.
Folkestone.
Grays, Essex.
Greenwich.
Hough, near Grantham.
Huntingdon.
Hurley Bottom, near Marlow, Berks.
Ilford.
Kew.
Lark's Hill, Balsham.
Lavenham, Suffolk.
Leigh, near Worcester.
Lexden, near Colchester.
Little Comberton, near Pershore, Worcestershire.
London, Cockspur Street.
London, Pall Mall.
Milton Street, also called Swanscombe, near Greenhithe, Kent.
Motcomb, Dorset.
Newmarket.
Overton, Yorks.
Oxford.
Peckham.
Piltdown, Sussex.
Reading (Kensington Road).
Tewkesbury.
Thame, Oxon.
Waterhouses, near Leek, Staffordshire.
Walton-on-the-Naze.
Wembley Park, Middlesex.
Whitstable, Kent.
Wortley, near Leeds.
Yarmouth (dredged off).

CAVES AND FISSURES.

Brixham, Devon.
Caldy Is., South Wales.
Cefn, near St. Asaph.
Cresswell Caves, near Chesterfield.
Durdham Down, Bristol.
Kent's Cave, Torquay.[2]
Kirkdale, Yorkshire.
Plymouth.
Pont Newydd, St. Asaph.
Ravenscliff, Gower.
Tor Bryan, Torquay.
Victoria Cave, Settle.

[1] 'Quart. Journ. Geol. Soc.,' xxv (1869), p. 192.

[2] Grave doubts were expressed by Ormerod ('Trans. Dev. Assoc.,' iii [1869], p. 79) and by Pengelly (*ibid.*, p. 483) as to whether the teeth of hippopotamus in the McEnery Collection supposed to have been found in Kent's cave really were found there. The British Museum, however, contains part of a jaw from the McEnery Collection from Kent's Cave.

Probably all the caves in which hippopotamine remains have been found were hyæna-dens, and it is a noteworthy fact that in almost every case the remains are chiefly those of calves or young adults. As Buckland, and after him Boyd Dawkins pointed out, it appears that it was only the young and inexperienced individuals that the hyænas were able to overcome and drag into their dens.

Boule[1] gives a map showing the distribution of the hippopotamus in Quaternary times. The area of distribution includes the south and east of England, practically the whole of France and Belgium, the Iberian Peninsula, Italy and Sicily, a small part of western Germany, North Africa, Syria and Cyprus. The author points out that a skeleton from Tiflis was found too late for this locality to be included in the map. The boundary in Britain is not drawn sufficiently far west to include the occurrences in the caves of North and South Wales.

By far the finest series of British hippopotamine remains is that from Barrington near Cambridge. The great majority of these are preserved in the Sedgwick Museum, Cambridge, others in the University Museum of Zoology and the British Museum. Next in importance is the series from Leeds preserved in the Leeds Philosophical Society's Museum. The British Museum contains a large series of bones from many localities, and there are others in the Museum of the Royal College of Surgeons and in the Bristol and Manchester Museums, and in the Museum of Practical Geology, Jermyn Street, London.

The distribution of the hippopotamus in Pleistocene times, and in particular its range as far north as York and its reported association with boreal animals like the mammoth, reindeer, and woolly rhinoceros, is a subject of much interest, and one to which many writers, including Lyell, Prestwich, Boyd Dawkins, J. Geikie and Boule have paid attention. There may be said to be three theories by which it has been sought to explain the facts.

(1) *That of Structural Modification.*—Prestwich[2] suggested that the palæolithic hippopotamus may have been protected by a hairy coat like *Rhinoceros tichorhinus* and the mammoth. As James Geikie points out, the hippopotamus is not the only animal concerned, as the contemporary *Elephas antiquus* and *Rhinoceros megarhinus* and *R. leptorhinus* would require similar protection, and it is hardly possible to believe that they were all provided with hairy coats.

(2) *That of Seasonal Migration.*—This theory has been most clearly expounded by Boyd Dawkins.[3] It is suggested that during a period of greatly contrasted seasons, when the climate was similar to that prevailing in some parts of Siberia and Canada at the present time, the southern forms like hippopotamus migrated northwards in the summer, while the northern forms like the mammoth migrated

[1] 'Les Grottes de Grimaldi,' iii, fasc. 3, p. 194.

[2] 'Phil. Trans.,' cliv (1864), p. 285.

[3] 'Pop. Science Review,' v (1871), p. 388.

southwards during the winter, and thus the two sets of bones became associated. This theory was proposed long before modern research had shown the existence of great fluctuations of climate during palæolithic times.

James Geikie opposed this theory on several grounds. For geographical and meteorological reasons he maintained that if the winter conditions in Britain were such as to produce a type of winter with cold comparable to that of Siberia, summer conditions would have been colder than in Siberia and the southern animals could not possibly have lived. Putting aside climatic considerations, he pointed out that the hippopotamus is not, properly speaking, a migratory animal. Lastly, the association of hippopotamine bones with shells like *Cyrena fluminalis* and *Unio littoralis*, which are not now found nearer Britain than North Africa, is inconsistent with the existence of very cold winters.

(3) *That of Climatic Change.*—This theory assumes that general changes of climate took place during the accumulation of the bone-bearing deposits. It was advocated in one form or another by nearly all the earlier writers on the subject, such as Lyell[1] and J. Geikie,[2] and is strongly supported by modern research. There are two modifications of it. According to J. Geikie the deposits containing *Hippopotamus* and other southern forms were accumulated during mild *interglacial* periods. By the majority of students of the subject the climatic changes are believed to be later than the main glaciation, the deposits with *Hippopotamus* being assigned to the Chelléan or oldest palæolithic stage. In the Riviera the hippopotamus survived to a later period, being found in Aurignacian caves near Mentone.

A fourth possible explanation of some at any rate of the cases in which southern and boreal forms are stated to be associated lies in error of observation or of determination. Boule[3] has laid much stress on this point. He shows that through error of observation bones which are in reality derived from an older deposit may be thought to be of the age of that in which they are found, while in other cases, *e.g.* the reported occurrence of the boreal form *Rhinoceros tichorhinus* with *Hippopotamus* at Barrington near Cambridge, the supposed association was due to wrong determination, the Barrington rhinoceros being *R. merckii*.

III. DESCRIPTION OF THE SKELETON.

The Hippopotamidæ agree with the other Suina, the pigs and peccaries, in the fact that the 3rd and 4th metacarpals and metatarsals remain distinct. The full series of 44 teeth is often present.

[1] 'Principles of Geology,' 10th ed., i, chap. 10. [2] 'Geol. Mag.,' ix (1872), p. 164.

[3] 'Bull. Soc. Géol. France,' [4], vii (1907), p. 382, and 'Les Grottes de Grimaldi,' i, fasc. 3 (1910), p. 194.

MEASUREMENTS OF CRANIUM.

	Skull (young adult) in Geol. Dept. of Brit. Mus.	Skull of old male, 1915, 2.3.1 in Zool. Dept. of Brit. Mus.	Skull of mounted skeleton from Bogoslav, Abyssinia, No. 726 in Zool. Dept. of Brit. Mus.	Skull No. 16.8.81 from Pongwa, Portuguese E. Africa, in Zool. Dept. of Brit. Mus.	Skull of old male (No. 1861) in Museum of R. Coll. of Surgeons.	Skull of mounted skeleton from Barrington in Sedgwick Mus., Cambridge.
Length from intercondylar notch to anterior end of skull	56·9	76·5	68·6	...	73·0	...
Extreme width across zygomatic arches	39·3	44·25	40·0	42·4	47·4	47·0
Width at narrowest part of skull in front of preorbital foramen	10·8	13·9	10·1	10·2	14·6	10·7
Measurement across orbits at fronto-lachrymal suture	21·2	26·85	21·15	21·9	27·3	24·3
Transverse measurement of cranium at its narrowest point behind orbits	12·9	12·9	12·4	12·25	14·6	11·3
Vertical height from intercondylar notch to top of sagittal crest	17·85	21·65	15·0	...	18·7	18·2
Transverse diameter of foramen magnum	6·8	7·5	6·0	...	4·9	6·0
Width of palate between M. 2	7·8	7·8	7·0	6·9	8·6	7·6
Width of posterior narial opening at pterygoid suture	8·0	5·9	5·85	3·7	5·5	7·0
Length of palate from posterior narial opening to point of divergence of premaxillæ	26·8	49·9	..	41·9	44·8	34·4

MEASUREMENTS OF MANDIBLE.

	Skull (young adult) in Geol. Dept. of Brit. Mus.	Skull of old male, 1915, 2.3.1 in Zool. Dept. of Brit. Mus.	Skull of mounted skeleton from Bogoslav, Abyssinia, No. 726 in Zool. Dept. of Brit. Mus.	Skull No. 16.8.81 from Pongwa, Portuguese East Africa, in Zool. Dept. of Brit. Mus.	Skull of old male (No. 1861) in Museum of R. Coll. of Surgeons.	Skull of mounted skeleton from Barrington, in the Sedgwick Mus., Cambridge.	Mandible from Barrington (1888), in the Sedgwick Mus., Cambridge.	Mandible from Barrington (1884), in the Sedgwick Mus., Cambridge.
Transverse measurement taken at the base of the canines	31·7	42·8	37·5	39·6	45·0	36·4	40·2	44·2
Transverse measurement across rami at posterior end of symphysis	21·3	26·2	25·2	24·2	26·8	25·3	26·5	24·5
Length of mandibular symphysis	17·3	20·0	16·7	19·2	21·1	17·7	18·55	19·2
Measurement across the antero-inferior projection of the angle	44·75	49·4	45·85	46·6	48·5	...	41·1	46·0
Width between ends of coronoid process	20·75	23·45	20·7	21·5	27·0	...	...	19·2
Width across condyles	35·2	40·8	34·25	36·2	40·6	34·0	...	35·6

The Hippopotamidæ differ from the other families in the broad and rounded character of the muzzle, in the larger size and persistent pulps of the canines and incisors, and in the fact that the digits are subequal, all reaching the ground in walking and being terminated by short rounded hoofs.

A. The Skull (Plates I—IV).

The brain cavity is very small, and the cranium little raised, so that a line drawn from the occipital crest to the nose is nearly parallel to the palate. The occipital crest is strongly developed, while there is a less marked sagittal crest which bifurcates in front to form two divergent ridges extending towards the orbits. The orbits are extremely prominent, particularly in old males, and project outwards and upwards. Postorbital processes from the frontals and jugals almost or quite meet and complete the postorbital bar. The lachrymal is peculiar; it occupies a relatively large space on the roof of the skull, while within the orbit it is dilated into a delicate thin-walled capsule. The lachrymal canal is deep within the orbit. The face contracts in front of the orbits and then expands into an enormous muzzle which lodges the huge incisor and canine teeth. The nasals, which are very long, are much widened at the posterior end, while anteriorly they diverge. The suborbital foramen is large. The palate is long and narrow, and the palatal aspect of the cranium is remarkable for the fact that the two series of teeth, instead of converging when followed forward, run parallel to one another or even diverge slightly. The hamular process of the pterygoid is frequently but not invariably prominent. There is a wide glenoid cavity formed by the squamosal, but the post-glenoid process is not very prominent. There is a very distinct paroccipital process of the exoccipital, but it is not nearly so prominent as in the pig. There is a long, narrow, auditory meatus terminating in an inconspicuous foramen. The mandible is immensely large and heavy with a long symphysis. It expands in front to lodge the great canine teeth, and in consequence is wider at the anterior than at the posterior end of the symphysis. The coronoid process is very small and somewhat recurved, while the angle is greatly expanded and bent outwards, ending in a downwardly and forwardly projecting process.

B. The Dentition (Plates V and VI).

The incisor and canine teeth of *Hippopotamus amphibius* are very remarkable, being immensely large and provided with persistent pulps. The grinding teeth on the other hand have a primitive bunodont character. The dental formula is i. $\frac{2}{2}$ c. $\frac{1}{1}$ pm. $\frac{4}{4}$ m. $\frac{3}{3}$.

The homology of the incisor teeth has been a matter of considerable difference of opinion. Owen[1] considered that the first and second incisors of both jaws were those represented; de Blainville,[2] on the other hand, writes: "Dans le très-jeune âge, il est certain qu'il y a trois paires d'incisives en haut comme en bas, et que ces incisives sont beaucoup plus subégales, dont une paire excessivement petite n'est pas remplacée, la première supérieurement, la troisième inférieurement." Lydekker,[3] arguing from the fact that $\overline{\text{i. 2}}$ in *H. palæindicus* is very small and apparently about to disappear, considered that this was the tooth which is missing in *H. amphibius* and that by analogy $\underline{\text{i. 2}}$ is also missing.

The following table shows the views of the various authorities on this point:

Owen and most authors considered the teeth represented to be .	$\underline{\text{i. 1 and 2}}$ and $\overline{\text{i. 1 and 2}}$
de Blainville considered the teeth represented to be . . .	$\underline{\text{i. 2 and 3}}$ and $\overline{\text{i. 1 and 2}}$
Lydekker considered the teeth represented to be	$\underline{\text{i. 1 and 3}}$ and $\overline{\text{i. 1 and 3}}$

De Blainville's statement as regards the lower milk-incisors is confirmed by an examination of a very young mandible (1873) in the Museum of the Royal College of Surgeons. In this mandible there are two small incisors, $\overline{\text{d.i. 1}}$ and $\overline{\text{d.i. 2}}$, and in the wide gap separating $\overline{\text{d.i. 2}}$ from the canine is an alveolus in which the germ of $\overline{\text{d.i. 3}}$ can be distinctly seen (Pl. V, fig. 17).

Another mandible in the Royal College of Surgeons Museum, that belonging to the skeleton (no. 1872) of a male hippopotamus two days old, shows a distinct pit in the position of $\overline{\text{d.i. 3}}$, but there is no tooth-germ in it. The germ might, however, easily have been lost in preparation. The wide gap separating the outer incisor from the canine in the adult skull also suggests that the tooth lost is the 3rd incisor. An examination of two young skulls in the College of Surgeons Museum, and of one in the Museum of Zoology at Cambridge, does not, however, lend any support to de Blainville's view that $\underline{\text{i. 1}}$ is the missing upper incisor in the adult. The very young skull (M. 10702) at Cambridge shows what is apparently the alveolus of $\underline{\text{d.i. 3}}$ between the canine and $\underline{\text{d.i. 2}}$. The skull of the male hippopotamus (no. 1872) two days old in the College of Surgeons Museum shows no trace of $\underline{\text{d.i. 3}}$. It seems best to adhere to the view ordinarily accepted that the missing incisors in the adult hippopotamus are $\underline{\text{i. 3}}$ and $\overline{\text{i. 3}}$. The fact that occasionally examples of *H. amphibius* are met with possessing three incisors should be noted, though this need not necessarily imply reversion. Falconer[4] refers to a specimen at Dublin with three incisors in the right mandible and two in the left, Gaudry[5] to a specimen at Paris with three incisors in the right and two in the left premaxilla.

Note.—Dr. C. W. Andrews very kindly examined the skulls at the Royal College of Surgeons Museum and agreed that in the mandible no. 1873 the germ of $\overline{\text{d.i. 3}}$ is present.

[1] 'Odontography,' p. 563.
[2] 'Ostéographie,' vii, p. 32.
[3] 'Palæont. Ind.,' iii, p. 48.
[4] 'Palæont. Mem.,' ii, p. 406.
[5] 'Bull. Soc. Géol. France,' [3], iv, p. 504.

Lydekker's conclusions with regard to the loss of incisors in the hippopotami are :

(*a*) That the earliest incisor teeth to disappear are i. 2 and i. 2.

(*b*) That when there is only one pair of incisors remaining, it is the first.

(*c*) That the disappearance of each pair of incisors takes place first in the lower jaw, later in the upper.

Order of Succession.—The last of the permanent teeth to appear is pm. 4, the last but one is m. 3. The earliest members of the permanent grinding series to appear are m. 1 and m. 1.

Permanent Dentition of the Upper Jaw (Plates V and VI).

The *incisor* teeth, which are straight, have considerably more than half their length concealed in the alveolus. Enamel is confined to their antero-external surfaces, and with use they assume a chisel-like form from friction with the corresponding teeth of the mandible. The postero-internal face is bevelled away.

I. 1, which is of even diameter throughout, is only slightly curved, and has the enamel extending over more than a quarter of its surface. A specimen in the Geological Department of the British Museum measures 10·75 cm. in length.

I. 2, which is more curved than i. 1, tapers towards its termination, which is somewhat sharply recurved. Here again only a quarter of the surface is coated with enamel.

C. (Text-fig. 1, A) is a much larger tooth and has nearly four-fifths of the surface enamel-coated, all in fact except the anterior face, which is bevelled away by friction with C. The canine projects further from the alveolus than the incisors. The posterior face of the tooth is marked by a prominent groove, the antero-internal surface by a feeble one.

The *premolars* are all conical teeth, and the interval between each and its successor decreases as the series is followed backwards. They vary considerably, and isolated examples of pm. 2 and 3 are difficult to distinguish from pm. 2 and 3.

Pm. 1 is a small tooth with a simple conical crown and a single root. In a large skull an interval of about 7·5 cm. commonly separates it from C. It is as a rule missing and its alveolus closed in old individuals. As it is cut very early and has no successor it is often considered to belong to the deciduous series and to be dm. 1.

Pm. 2 is a much larger tooth than pm. 1, with an elongated conical crown and two roots. In some cases there is little indication of a cingulum, in others it is fairly well marked.

Pm. 3 is a still larger tooth similar in character to pm. 2, but always with a strongly developed cingulum on its posterior and inner borders.

Pm. 4 retains in the main the conical form of the other premolars, but is a shorter and stouter tooth, with a strongly marked cingulum. The main cone has a ridged surface, and when worn the enamel may have a pentagonal outline (Pl. V, fig. 8). Examination of recent skulls shows the tooth to vary considerably. Pm. 4 cuts the jaw considerably later than pm. 3 and is consequently less worn in most skulls.

The three *molars* are semiquadrate teeth with the same general type of structure, and are typically bunodont and marked by a strong cingulum. In each a transverse groove divides the crown into two prominent cones, each of which is further subdivided by a longitudinal groove. The outline of the enamel in the worn tooth is strongly lobate (Pl. VI, fig. 3). Each tooth has four powerful roots which diverge somewhat and hold it firmly in the jaw. M. 1 is always more worn than m. 2, and m. 2 than m. 3. Unworn molar teeth that have not cut the jaw are difficult to distinguish from one another.

M. 1 has the cingulum swelling into a small tubercle on the outer surface opposite the transverse groove, and a less marked swelling at a corresponding position on the inner side of the tooth.

In M. 2 the cingulum may rise into a fairly prominent tubercle on the outer side of the tooth, but not on the inner side.

M. 3 has the cingulum rising into a rather marked posterior tubercle, while there may be slight swellings of the cingulum opposite both inner and outer ends of the transverse valley.

The worn molars are well described in Tomes' 'Dental Anatomy'[1] as follows: "These latter, especially when worn, have a very characteristic double trefoil pattern; the four cusps in the first instance were separated by a deep longitudinal and still deeper transverse groove; each cusp was, moreover, trilobed. The first result of wear is to bring out the appearance of four trefoils. Next, when the longitudinal furrow is worn away four lobed figures result, and finally all pattern becomes obliterated and a plain field of dentine surrounded by enamel alone remains."

Permanent Dentition of the Lower Jaw (Plate V).

The lower *incisors* are implanted more horizontally in the jaw than the upper, and are in consequence more forwardly directed.

I. 1 (Text-fig. 1, B) is a very large tooth with, as a rule, half its length projecting from the alveolus. The whole surface is coated with a thin layer of enamel. Friction with i. 1 causes the upper (posterior) surface to be worn away somewhat irregularly, but chiefly externally.

[1] 7th ed., p. 514.

Fig. 1.—A left $\underline{C}$. seen from inner side: B right $\overline{i.1}$ and C right $\overline{i.2}$ seen from the outer side; D right $\overline{C}$. seen from the outer side. All $\frac{1}{2}$ natural size. From Barrington and preserved in the Sedgwick Museum, Cambridge.

I. 2 (Text-fig. 1, C) is a very much smaller tooth with only about 3 cm. projecting from the alveolus in a full-grown skull. Friction tends to reduce it to a somewhat conical form, the postero-internal and external surfaces being bevelled away.

C (Text-fig. 1, D) is a very large tooth, far larger than c. In cross-section it is triangular; the base of the triangle, which is the shortest of the three sides, is posterior. This face consists of dentine only, while the other sides are somewhat thickly coated with enamel marked by shallow longitudinal grooves.

The *premolars* have a general similarity to those of the upper jaw.

Pm. 1 is a small one-rooted tooth which falls out early.

Pm. 2 is a conical tooth with two strong divergent roots. There is a slight cingulum developed on the anterior and inner faces. This tooth is sometimes missing and its alveolus closed in a very old skull.

Pm. 3 and 4 are of the same type, but somewhat larger and with the cingulum better developed, especially in pm. 4.

The *molars* are very like those of the upper jaw, especially as regards the thickness of the enamel, but they do not show much tendency to the development of small cusps at the ends of the transverse valleys bisecting the tooth.

M. 1 and 2 have four roots. The cingulum is less marked than in the corresponding teeth of the upper jaw.

M. 3 has five roots. It is the largest of the molar teeth and the only one possessing a well-marked posterior cone.

Milk Dentition (Plate VI).

The formula of the *milk* dentition is :—di. $\frac{3}{3}$ dc. $\frac{1}{1}$ dm. $\frac{4}{4}$.

Milk Dentition of the Upper Jaw.

The milk-*incisors* are minute, subequal, conical teeth, with a complete enamel cap.

The *canine* is a little conical tooth, in character similar to the incisors, and only very slightly larger.

Of the milk-molars dm. 1 is unrepresented unless the tooth here regarded as pm. 1 is really dm. 1. Dm. 2 is a simple conical tooth with two widely divergent roots. There is a minute cusp placed postero-internally to the principal cone. Dm. 3 is a considerably larger tooth and more triquetral—wider behind. It consists of an anterior cone preceded by a small cusp and separated by a deep valley from a bilobed posterior cone. "After prolonged wear it shows four distinct enamel lobes, two longitudinal in front and two transverse behind" (de Blainville). Dm. 4 is a much larger tooth, resembling the permanent molars. It is divided by a deep transverse valley into anterior and posterior sections, each of which in the unworn tooth is bicuspid. There are four strong roots. The enamel of the worn tooth shows a kind of trefoil as in the adult molars.

Milk Dentition of the Lower Jaw.

The milk-*incisors* and *canines* are very small conical teeth, much like those of the upper jaw. $\overline{\text{Dm. 1}}$ is unrepresented unless the tooth here regarded as $\overline{\text{pm. 1}}$ is really $\overline{\text{dm. 1}}$.

$\overline{\text{Dm. 2}}$ is a simple conical tooth, with a rectangular outline. When unworn it may have two minute cusps placed behind the principal cone. The roots diverge strongly.

$\overline{\text{Dm. 3}}$ is bigger and has a large anterior cone preceded by a small cusp and divided by a deep furrow from a bilobed posterior cone. There is a fairly well-marked cingulum, and two roots are present behind and one in front.

$\overline{\text{Dm. 4}}$ is a larger tooth with three large bifid cones divided from one another by deep grooves. Slight cusps occur in front of the first cone and larger cusps behind the third. There are a single anterior and two posterior roots.

Measurements of Certain Permanent Teeth.

	Skull 1915, 2.3.1 in Zool. Dept. of the Brit. Mus.	Skull 1861 in Roy. Coll. of Surgeons Mus.	Separate tooth, 1899*a*, in Roy. Coll. of Surgeons Mus.	Anterior half of mandible, Sedgwick Mus., Cambridge (pres. Evans).	Largest isolated tooth from Barrington (figd.), in Sedgwick Mus., Cambridge.
Length of $\underline{\text{C}}$.		.	...	. .	30·0*
Length of $\overline{\text{I. 1}}$	...	...	...	...	37·5
Length of extra-alveolar portion of $\overline{\text{I. 1}}$	30·25	25·4	...	27·45	...
Length of $\overline{\text{C}}$. measured along anterior curvature	...	...	84·5	...	74·0
Length of extra-alveolar portion of $\overline{\text{C}}$.	21·5	25·9	...	40·4*	...
Length of extra-alveolar portion of $\overline{\text{I. 2}}$	8·55	9·4	...	6·4	...

* Measured along anterior curvature.

c. The Vertebral Column. (Text-figures 2–7.)

Cervical Vertebræ.—The *atlas* (Text-fig. 2, A, B) has a very large articulating surface for the axis and broad transverse processes thickened at their distal ends.

The *axis* (Text-fig. 2, C) has a blunt odontoid process and a very large articulating surface for the atlas. The neural spine varies considerably; sometimes it is elevated posteriorly and slopes steeply down anteriorly, sometimes it has an evenly rounded crest and is nearly as much elevated anteriorly as posteriorly. The transverse processes are well marked.

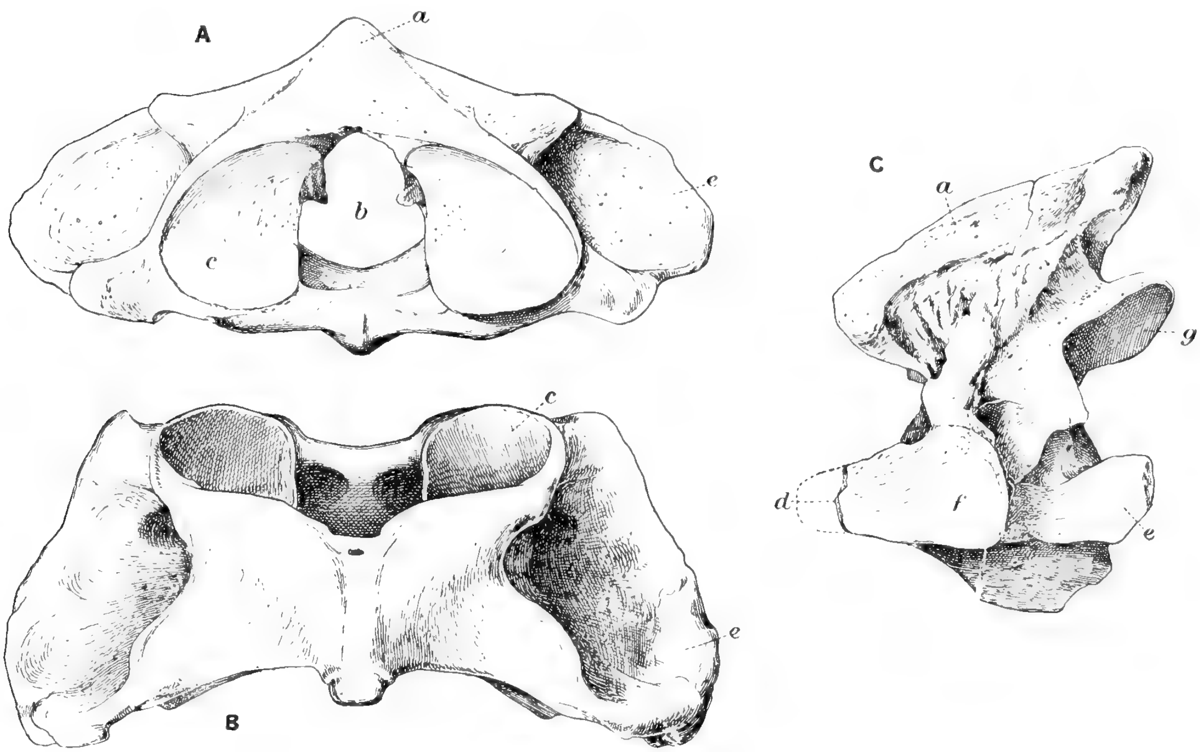

Fig. 2.—A Atlas, front view: B Atlas, seen from above; C Axis, left side view. All ⅓ natural size. All from Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, neural spine; *b*, neural canal; *c*, surface for articulation with condyles of skull; *d*, odontoid process (broken); *e*, transverse process; *f*, surface for articulation with atlas; *g*, postzygapophysis.

The remaining *cervicals* (Text-fig. 3) have the anterior surface of the centrum, which retains all through the series a very uniform length, very slightly convex, and the corresponding posterior surface very slightly concave. The transverse processes are prominent and have descending flanges, which increase somewhat in size in the later vertebræ. The seventh is, however, without a descending flange. The neural spines, except that of the seventh, are of no great size and increase gradually in height as the series is followed back. Those of the sixth and seventh are slightly turned forward, and that of the seventh may be much longer than that of the sixth.

MEASUREMENTS OF CERVICAL VERTEBRÆ.

	Mounted skeleton in Zool. Dept. of Brit. Mus. (726w)	Mounted skeleton In Sedgwick Mus., Cambridge.	Set of mounted vertebræ in Zool Mus., Cambridge.
ATLAS.			
1. Maximum width ...	29·1	35·3	29·7
2. Median dorso-ventral diameter ...	10·75	15·8	11·05
3. Extreme width of condylar articular surface ...	14·75	18·2	15·5
AXIS.			
1. Length from anterior end of odontoid process to postero-ventral extremity of centrum ...	13·15	14·75	15·6
2. Height from base of centrum to top of neural spine ...	14·55	21·5	16·1
3. Height from roof of neural canal to top of neural spine ...	5·2	9·5	6·0
4. Diameter across transverse processes ...	17·3	19·65	18·5
5. Diameter across articulating surfaces for atlas ...	16·7	17·75	15·65
6. Diameter across postzygapophyses ...	10·6	13·3	10·0

	3rd Cervical.			4th Cervical.			5th Cervical.			6th Cervical.			7th Cervical.		
	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Sedgwick Mus., Cambridge.	Set of mounted vertebræ in the Zool. Mus., Cambridge.	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Sedgwick Mus., Cambridge.	Set of mounted vertebræ in the Zool. Mus., Cambridge.	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Sedgwick Mus., Cambridge.	Set of mounted vertebræ in the Zool. Mus., Cambridge.	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Sedgwick Mus., Cambridge.	Set of mounted vertebræ in the Zool. Mus., Cambridge.	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Sedgwick Mus., Cambridge.	Set of mounted vertebræ in the Zool. Mus., Cambridge.
1. Width across transverse processes ...	22·2	24·4	23·6	21·75	23·8	23·1	21·5	23·6	21·25	20·1	23·5	20·8	19·75	21·9	20·2
2. Width across postzygapophyses ...	11·55	11·4	12·0	11·85	11·7	12·15	12·1	12·4	12·75	13·0	14·0	12·5	13·1	14·65	12·0
3. Height from roof of neural canal to top of neural spine ...	5·2	5·9	5·8	5·1	6·55	6·1	6·1	7·35	8·0	6·6	9·2	10·5	8·85	11·5	18·65
4. Length of inferior lamella of transverse process ...	6·9	7·4	9·9	7·8	...	9·15	9·7	8·8	9·4	12·05	12·15	10·1	...	...	...

Thoracic Vertebræ (Text-fig. 4).—These number 14 or 15. The neural spines of the anterior vertebræ are long, though the length varies considerably in different individuals; they decrease gradually in length as far as the anticlinal vertebra, which is the last but one. The longest spines are considerably shorter than those of a rhinoceros of corresponding size. The inclination of the neural spines from the vertical gradually increases from the first, where the spine is almost vertical, to the

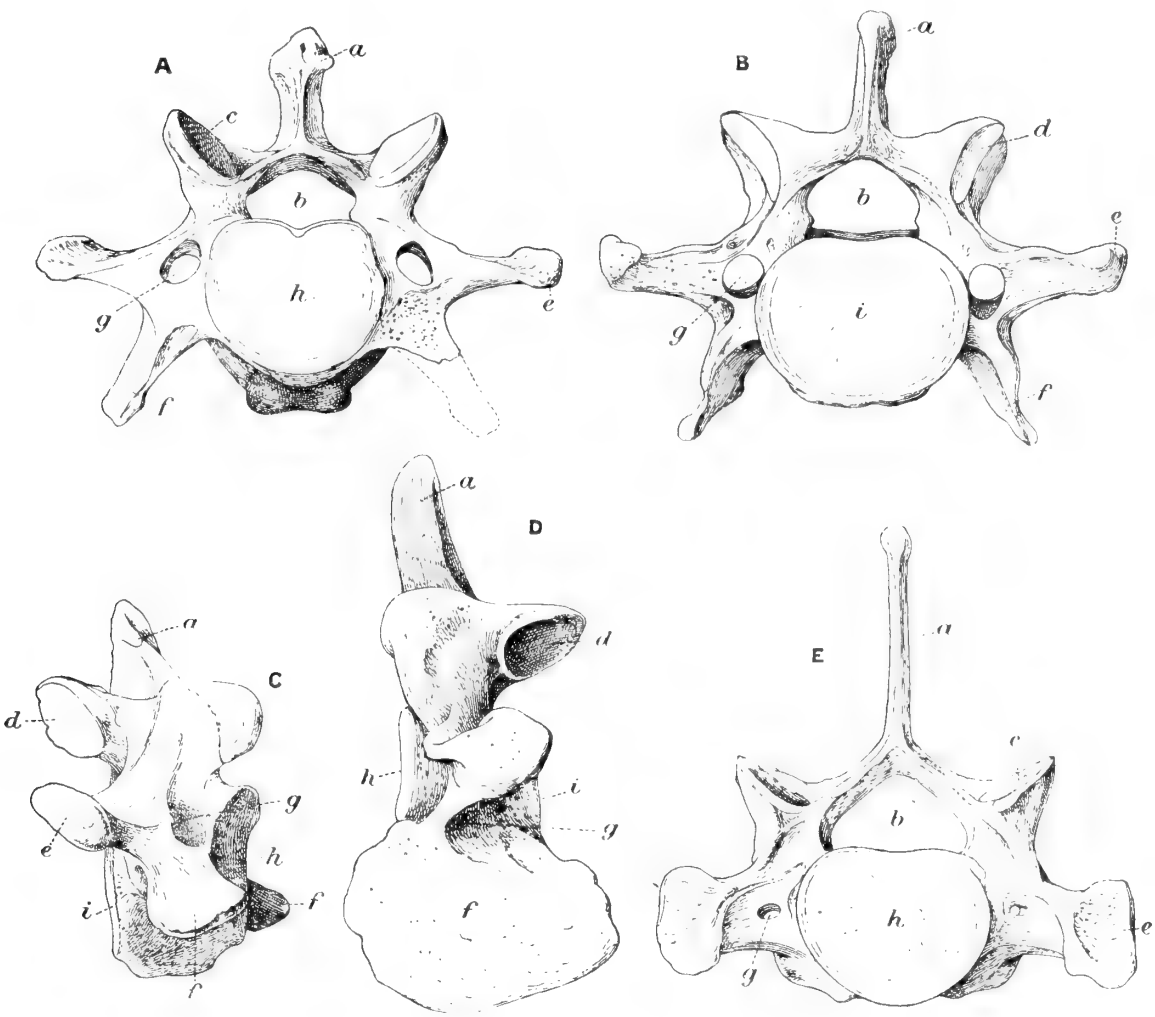

Fig. 3.—Cervical vertebræ. A 4th, front view; B 5th, posterior view; C 3rd, right side view; D 6th, left side view; E 7th, front view. All ¼ natural size. All from Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, neural spine; *b*, neural canal; *c*, prezygapophysis; *d*, postzygapophysis; *e*, transverse process; *f*, inferior lamella of transverse process; *g*, vertebrarterial canal; *h*, anterior face of centrum; *i*, posterior face of centrum.

eighth. The short stout spines of the last four or five vertebræ gradually become more and more nearly vertical. The centra are nearly cylindrical, have flat articulating surfaces, and are very uniform in length. The zygapophyses lie horizontally as far back as the 10th or 11th vertebræ, after which they become almost vertical, as in the lumbars.

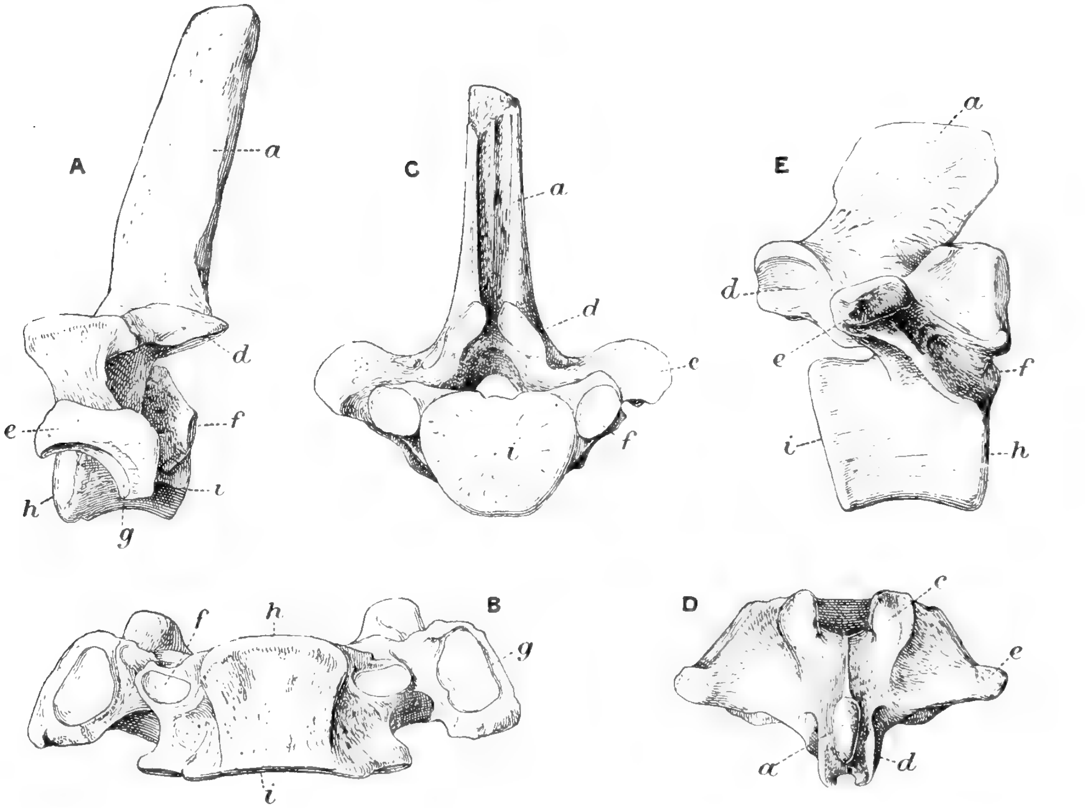

Fig. 4.—Thoracic vertebræ. **A** 1st, left side view; **B** 1st, seen from below; **C** 4th, seen from behind; **D** 12th, seen from above; **E** 15th, seen from right side. All ¼ natural size. All from Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, neural spine; *b*, neural canal; *c*, prezygapophysis; *d*, postzygapophysis; *e*, transverse process; *f*, surface for articulation with head of rib; *g*, surface for articulation with tubercle of rib; *h*, anterior face of centrum; *i*, posterior face of centrum.

Measurements of Thoracic Vertebræ.

	1st.	4th.		7th.	10th.	12th.		15th = 1st lumbar.	
	Set of mounted vertebræ in Zool. Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Barrington, Sedgwick Mus., Cambridge (figd.).	Set of mounted vertebræ in Zool. Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Barrington, Sedgwick Mus., Cambridge (figd.).	Set of mounted vertebræ in Zool. Mus., Cambridge.	Barrington, Sedgwick Mus., Cambridge.
1. Height from notch between prezygapophyses to top of neural spine	23·1	23·3	16·25	19·65	10·5	9·3	8·4	9·4	10·6
2. Width across transverse processes	19·75	15·05	19·1	15·7	15·6	17·15	17·5	26·5	27·8
3. Width across prezygapophyses	12·4	7·15	...	...	7·2	5·55	...	6·6	...

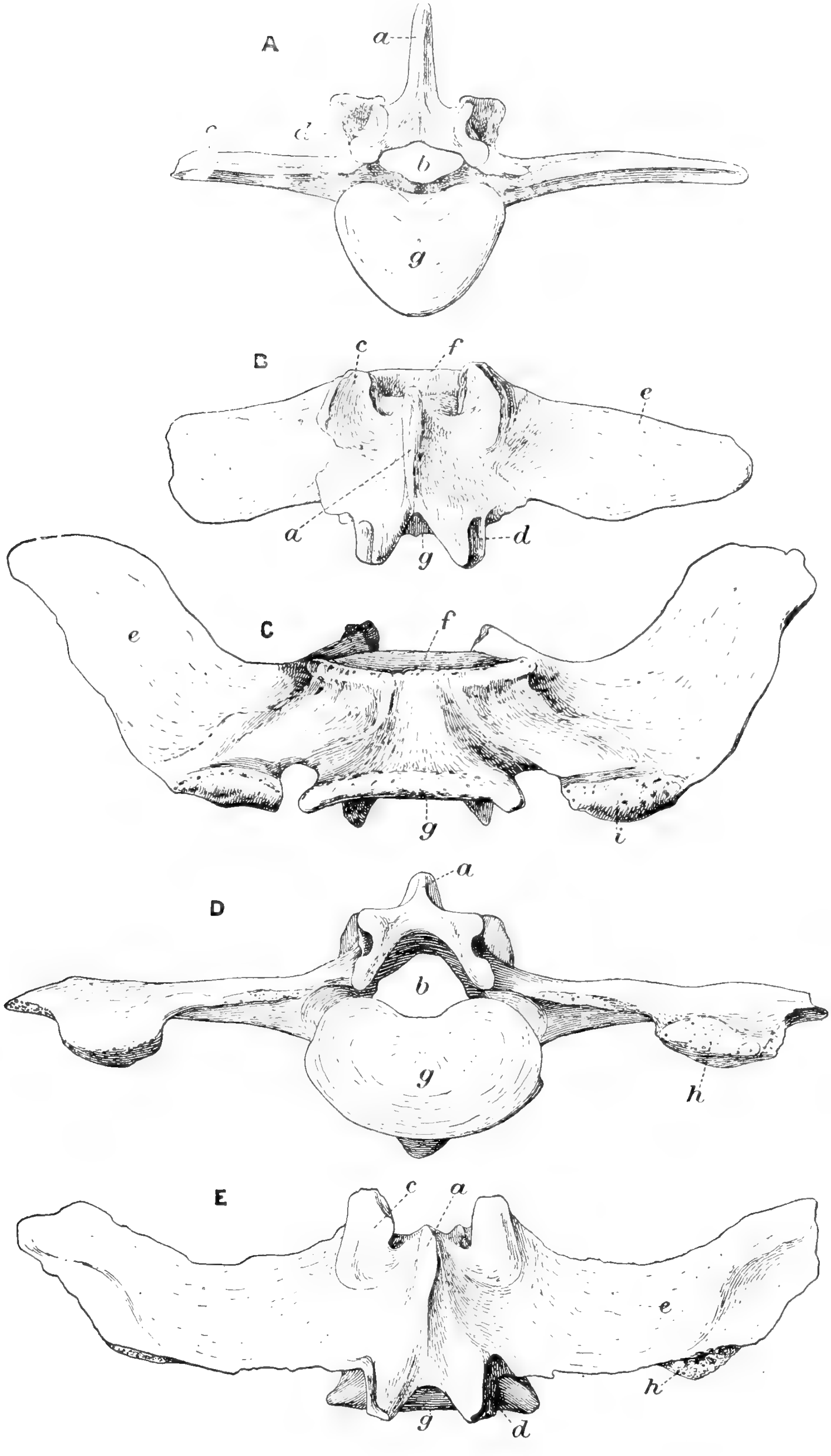

FIG. 5.—Lumbar vertebræ. **A** 3rd, seen from behind; **B** 3rd, seen from above; **C** 4th (last) seen from below; **D** 3rd (abnormal), seen from behind; **E** 3rd (abnormal), seen from above. All ¼ natural size. All from Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, neural spine; *b*, neural canal; *c*, prezygapophysis, or process bearing it; *d*, postzygapophysis; *e*, transverse process; *f*, anterior face of centrum; *g*, posterior face of centrum; *h*, extra articulating surface on tranverse process of abnormal vertebra; *i*, articulating surface for 1st sacral.

Lumbar Vertebræ (Text-fig. 5).—These are sometimes five, sometimes four in number. All have short, squarely truncated neural spines, that of the 1st=15th thoracic being vertical, those of the others slightly forwardly-directed. The transverse processes of the first are small, those of the other vertebræ very wide and flattened, and with their ends somewhat forwardly-directed, especially in the case of the last two. The centra are slightly procœlous. The last lumbar has its transverse processes articulating by a large rounded surface with the first sacral; its centrum is much depressed. The lumbar vertebræ of *Rhinoceros* differ completely in the longer, narrower and more backwardly-directed neural spines and in the small size of the transverse processes. While the penultimate lumbar vertebra is as a rule similar to the antepenultimate, having a high neural spine, a deep centrum and broad unthickened transverse processes, a specimen from Barrington collected by Dr. Poignand in 1900 simulates the characters of the last vertebra, the length of the neural spine and depth of the centrum are much reduced, and each transverse process bears postero-ventrally a large rounded surface which articulates with the end of the transverse process of the last vertebra. These rounded surfaces are situated about two-thirds of the distance from the centrum to the end of the transverse process.

MEASUREMENTS OF LUMBAR VERTEBRÆ.

	1st.			2nd.			3rd.				4th.		
	Mounted skeleton of adult female (1858) in Roy. Coll. of Surg. Mus.	Mounted skeleton Sedgwick Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Mounted skeleton of adult female (1858 in Roy. Coll. of Surg. Mus.	Mounted skeleton, Sedgwick Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Mounted skeleton of adult female (1858) in Roy. Coll. of Surg. Mus.	Mounted skeleton, Sedgwick Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.	Barrington, Sedgwick Mus., Cambridge (figd.).	Mounted skeleton of adult female (1858) in Roy. Coll. of Surg. Mus.	Mounted skeleton, Sedgwick Mus., Cambridge.	Set of mounted vertebræ in Zool. Mus., Cambridge.
1. Length of centrum ...	8·1	8·6	7·65	8·1	8·5	8·1	8·6	9·35	8·5	8·4 8·9*	6·8	8·6	7·55
2. Measurement across transverse processes	35·8	44·0	38·5	42·8	48·0	48·5	46·8	47·0	51·4	40·0 44·1*	44·6	50·8	42·5
3. Height from mid-ventral point of centrum to top of neural spine	16·2	19·75	17·4	17·7	20·9	17·9	18·0	21·0	17·55	18·95 15·0*	15·9	20·05	14·9
4. Height of centrum at posterior margin ...	...	...	5·9	..	...	5·9	...	...	5·3	7·2 6·1*	...	...	4·65

* These measurements are those of the abnormal vertebra described above.

Sacral and Caudal Vertebræ (Text-figs. 6 and 7).—There are two true sacral vertebræ, but the three or four anterior caudal vertebræ are ankylosed with them, together forming a long sacrum, much like that of the pig and differing strongly

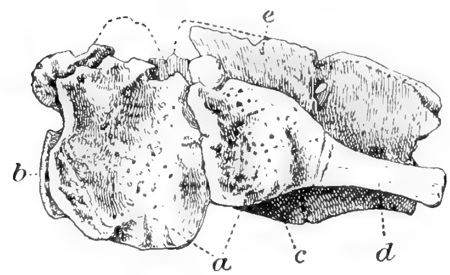

FIG. 6.—Sacrum. ¼ natural size. From Barrington, preserved in the Sedgwick Museum, Cambridge. *a*, articular surface for ilium; *b*, anterior face of centrum of 1st sacral vertebra; *c*, centrum of 2nd sacral vertebra; *d*, transverse process of 1st caudal (1st pseudo-sacral) vertebra; *e*, neural spine of 2nd sacral vertebra.

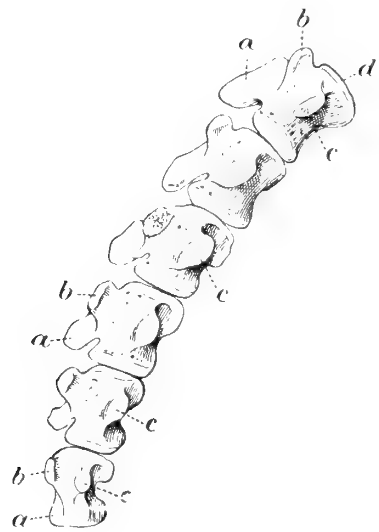

FIG. 7.—Free caudal vertebræ, mounted in the skeleton made up of bones from Barrington in the Sedgwick Museum, Cambridge. ¼ natural size. *a*, neural spine; *b*, metapophysis; *c*, transverse process; *d*, anterior face of centrum of 7th caudal (4th free caudal).

MEASUREMENTS OF SACRAL AND CAUDAL VERTEBRÆ.

	Mounted skeleton 726 n in Zool. Dept. of Brit. Mus.	Separate sacrum from Barrington, Sedgwick Mus., Cambridge (figd.).	Sacrum associated with pelvis from Barrington, Sedgwick Mus., Cambridge (figd.).
1. Length of sacrum	27·1	..	33·4
2. Height to top of neural spine of 2nd true sacral	8·3	10·6	11·0
3. Measurement across transverse processes of 2nd caudal (pseudo-sacral)	10·3	.	.
4. Measurement across transverse processes of 7th caudal (3rd free caudal)	11·0		.

from that of the rhinoceros. The ankylosed caudal (pseudo-sacral vertebræ) have short rounded neural spines and broad wing-like transverse processes which unite one with another distally. There are about fourteen free caudal vertebræ, the anterior of which have low neural spines like those of the sacrals, and rather long, narrow flattened transverse processes.

D. The Ribs and Sternum.

The *ribs*, of which there are fifteen pairs, have the broad flattened form so characteristic of Ungulates. Almost the whole trunk is embraced by them. Six pairs meet the sternum, being connected with it by imperfectly ossified sternal ribs, which rapidly increase in length as the series is followed back.

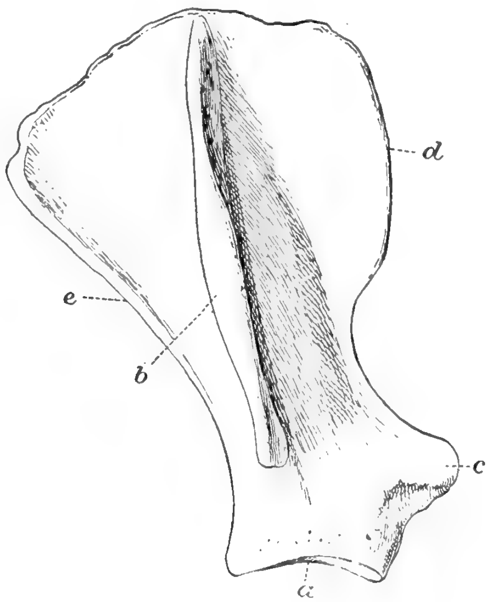

Fig. 8.—Right scapula seen from the outer side. ¼ natural size. From Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, glenoid cavity; *b*, spine; *c*, coracoid process; *d*, coracoid border; *e*, glenoid border.

There is a large compressed and keeled *presternum* bearing a pair of juxtaposed facets for articulation with the first pair of ribs. The *mesosternum* consists of four segments, the first being laterally compressed, the last two dorso-ventrally. The second is laterally compressed in front, but wide behind. The ossified part of the *xiphisternum* is narrow and pointed, but it terminates in a broad cartilaginous plate.

E. The Shoulder Girdle. (Text-figure 8.)

The *scapula* (Text-fig. 8) has a strong spine, but the acromion is not prominent. The coracoid process is well marked and slightly hooked and upturned.

MEASUREMENTS OF THE SCAPULA.

	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Mounted skeleton in Zool. Mus., Cambridge.
1. Length along line of spine	43·5	40·0
2. Maximum width	26·8	26·8
3. Width at neck	9·7	9·2
4. Width at proximal end measured from end of coracoid process.....................	15·95	16·3

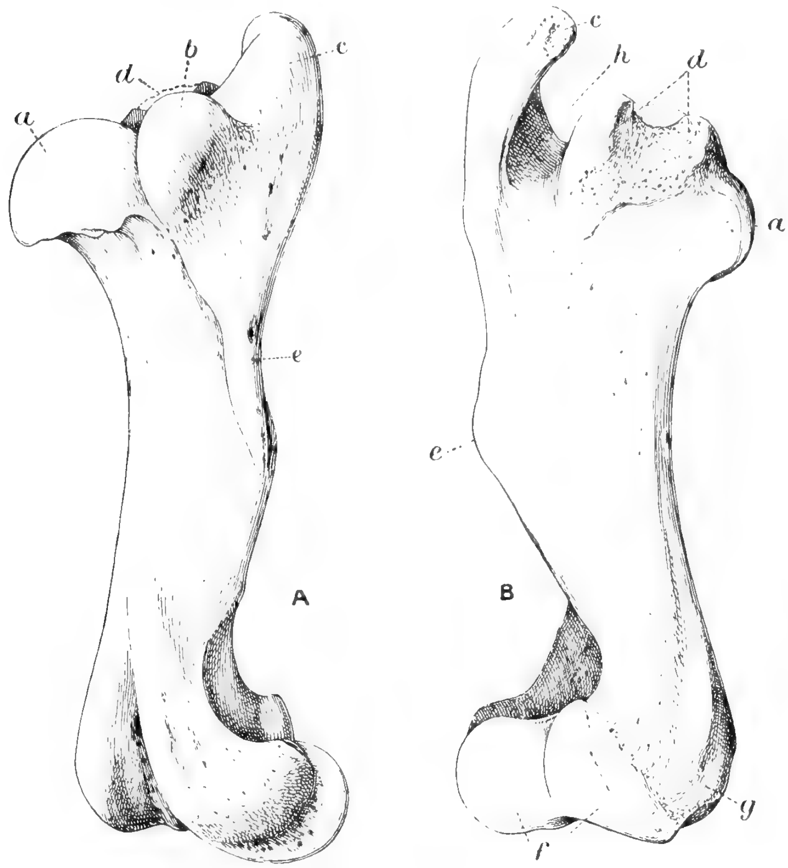

FIG. 9.—Right humerus of skeleton made up of bones from Barrington, mounted in the Sedgwick Museum, Cambridge. ¼ natural size. **A** outer view. **B** antero-internal view. *a*, head; *b*, great (outer) tuberosity; *c*, process from great tuberosity; *d*, lesser tuberosity; *e*, deltoid ridge; *f*, trochlear surface; *g*, internal condyle.

F. THE ANTERIOR LIMB. (Text-figures 9–11.)

In the *humerus* both the tuberosities are strongly developed, and there is a marked deltoid ridge. The great tuberosity is drawn out into a powerful process slightly inwardly directed. The condyle is strongly marked, and there is a very large anconeal fossa, but no supratrochlear foramen or conspicuous supinator ridge.

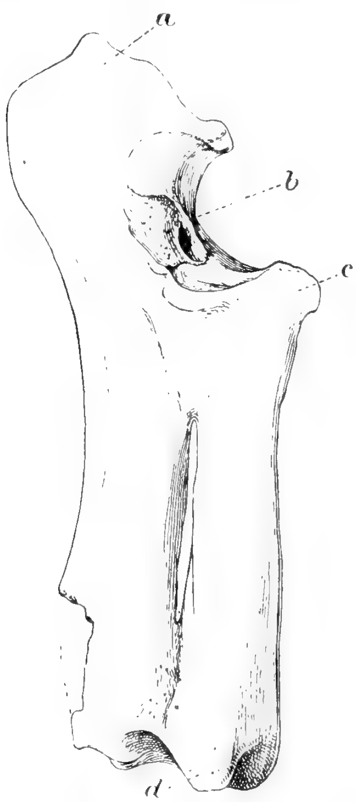

FIG. 10.—Antero-external view of right radio-ulna of skeleton made up of bones from Barrington, mounted in the Sedgwick Museum, Cambridge. ¼ natural size. *a*, olecranon; *b*, surface for articulation with trochlea; *c*, proximal end of radius; *d*, distal end of radius.

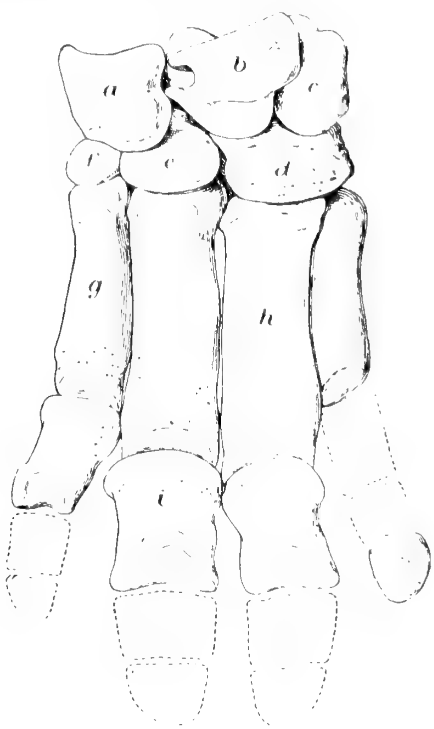

FIG. 11.—Front view of left manus of skeleton made up of bones from Barrington, mounted in the Sedgwick Museum, Cambridge. ¼ natural size. *a*, scaphoid; *b*, lunar; *c*, cuneiform; *d*, unciform; *e*, magnum; *f*, trapezoid; *g*, 2nd metacarpal; *h*, 4th metacarpal; *i*, proximal phalanx of 3rd digit.

The *radius* and *ulna* do not greatly differ in thickness, and are commonly firmly ankylosed together in the adult. The radius is a stout bone with both ends considerably expanded. The ulna has a strong keel running along the posterior face from the large olecranon.

The three proximal bones of the *carpus* are fairly equal in size. The scaphoid and lunar articulate entirely with the radius, the cuneiform entirely with the ulna. The distal row of carpals includes four bones, the large unciform articulating with the cuneiform and lunar, the magnum with the lunar and scaphoid. The small trapezoid articulates with the scaphoid, while a small trapezium articulates only with the trapezoid.

There are four *digits* (the pollex being absent), all very similar in character and length, and each consisting of a distinct metacarpal and three phalanges. The ungual phalanges are broad and rounded in front.

TABLE OF MEASUREMENTS.

	Mounted skeleton 726h in Zool. Dept. of Brit. Mus.	Mounted skeleton from Barrington in Sedgwick Mus., Cambridge (rt.).	Separate bones mounted in Zool. Mus., Cambridge.
HUMERUS.			
1. Extreme length	43·6	47·2	42·2
2. Maximum transverse diameter at distal end	13·4	14·5	13·75
3. Antero-posterior diameter of shaft at highest point in deltoid ridge	9·1	11·55	9·8
RADIUS.			
1. Extreme length	27·7	31·9	26·5
2. Width at proximal end	10·4	11·0	10·0
3. Width at distal end	10·6	11·0	10·8
4. Width at narrowest part of shaft	4·85	5·0	4·65
ULNA.			
1. Extreme length	38·3	42·0	39·0
2. Antero-posterior diameter at middle of shaft	6·9	5·5	6·5
METACARPALS.			
Length of metacarpal 2	13·1	...	..
" " 3	16·3	..	...
" " 4	14·0	...	...
" " 5	10·85	...	...

G. THE PELVIC GIRDLE. (Text-fig. 12.)

The pelvis is elongated and not specially large in proportion to the size of the animal. Its long axis approaches more nearly to the horizontal than in *Rhinoceros* or ruminants. The *ilium*, which is much expanded at the upper (anterior) end, differs from that of *Rhinoceros* in being more squarely truncated on both inner and outer edges and in being less concave upwards. Between the expanded portion and the acetabulum the ilium is much contracted. There is a long symphysis including a considerable part of the *ischium*, which is long and expanded posteriorly. The

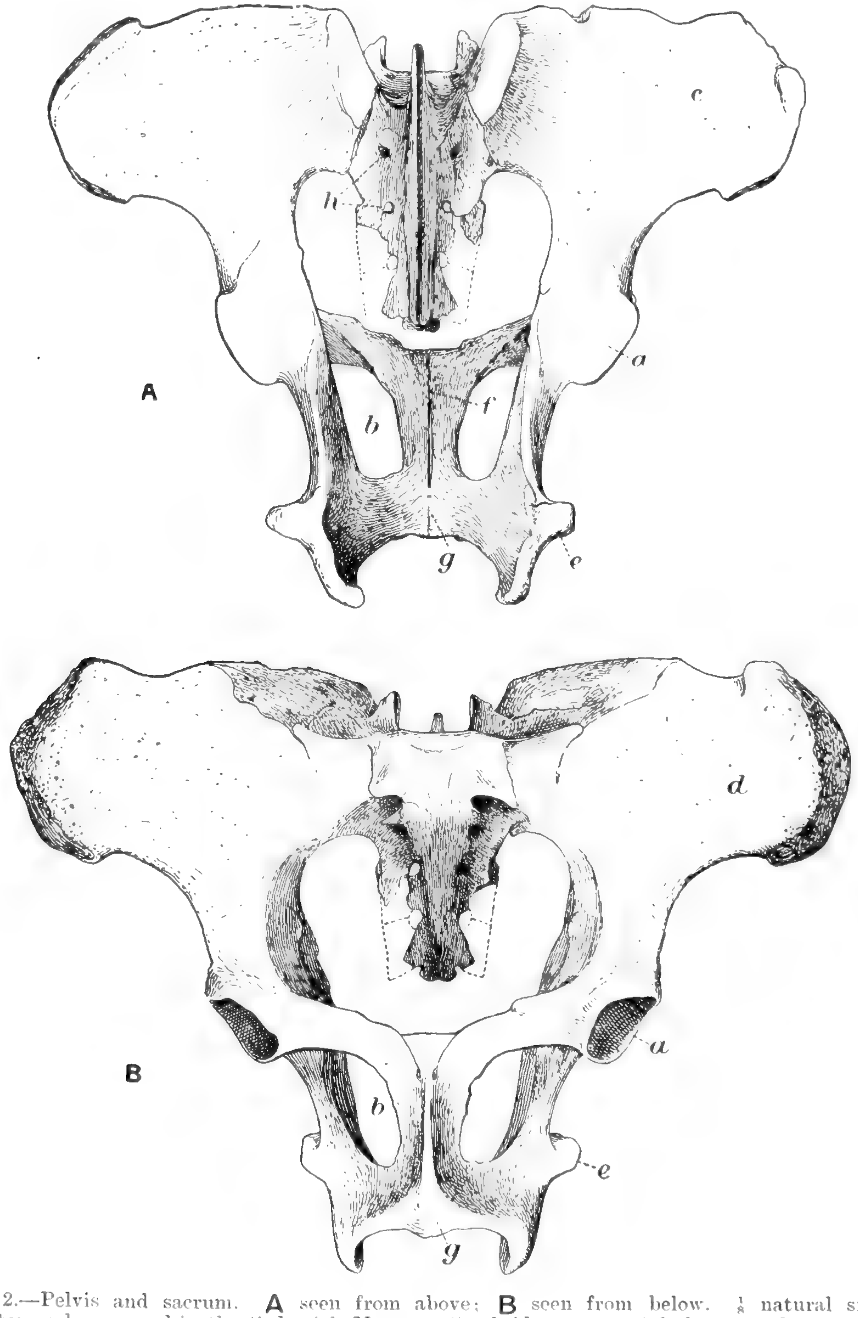

Fig. 12.—Pelvis and sacrum. **A** seen from above; **B** seen from below. ⅛ natural size. From Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, acetabulum; *b*, obturator foramen; *c*, gluteal surface of ilium; *d*, iliac surface of ilium; *e*, ischial tuberosity; *f*, pubic symphysis, *g*, ischial symphysis; *h*, foramen for exit of spinal nerve.

ischial tuberosities are not so prominent as in ruminants. The obturator (thyroid) foramen is large and regularly oval, not nearly circular as in *Rhinoceros*.

MEASUREMENTS OF THE RIGHT INNOMINATE BONE.

	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Separate pelvis from Barrington in Sedgwick Mus. Cambridge.
1. Maximum length	67·55	78·3
2. Length from acetabulum to supra-iliac border of ilium	34·0	39·45
3. Width of expanded anterior portion of ilium	33·0	44·4
4. Width of ilium at narrowest point in front of acetabulum	10·0	12·5
5. Antero-posterior measurement of obturator foramen	15·0	15·95
6. Transverse measurement of obturator foramen	8·9	10·1
7. Length of symphysis	20·5	26·0*
8. Depth of ischium from symphysis to end of tuberosity	21·4	30·0

* Partly by estimation.

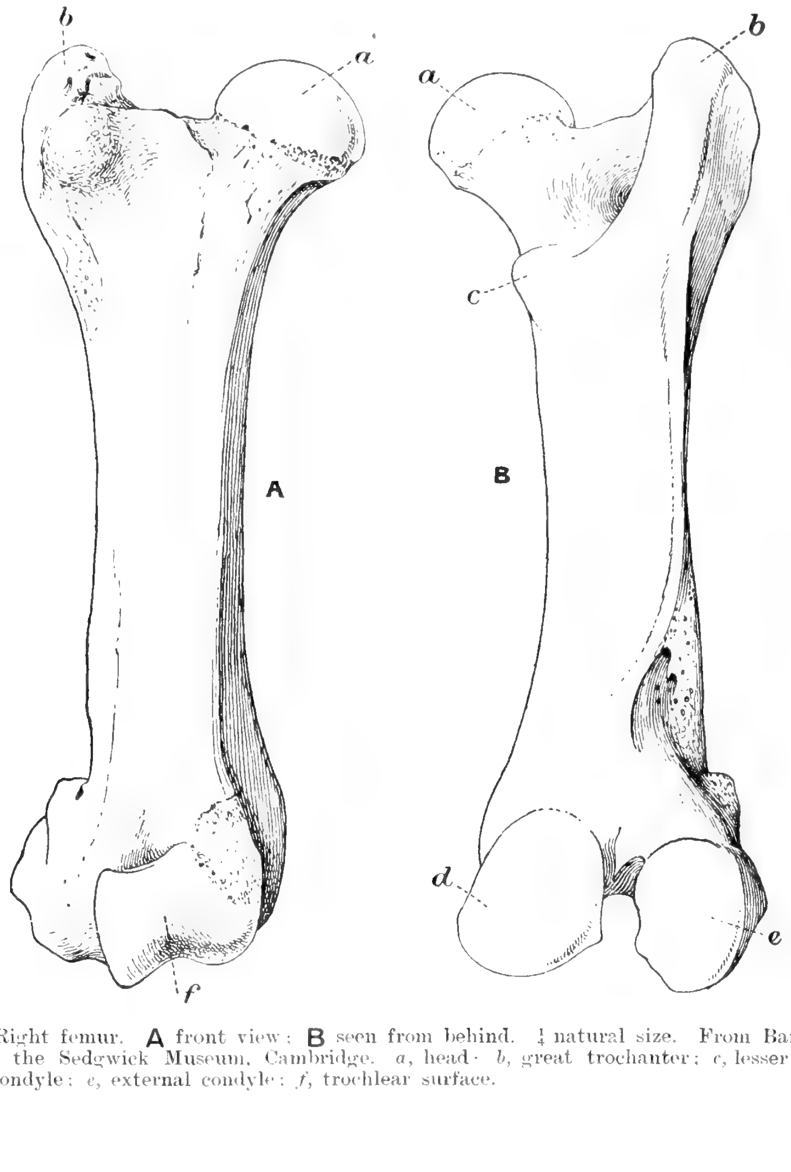

FIG. 13.—Right femur. A front view; B seen from behind. ¼ natural size. From Barrington and preserved in the Sedgwick Museum, Cambridge. *a*, head; *b*, great trochanter; *c*, lesser trochanter; *d*, internal condyle; *e*, external condyle; *f*, trochlear surface.

H. THE POSTERIOR LIMB. (Text-figures 13–16.)

In the *femur* there is a distinct neck separating the prominent rounded head from the rest of the bone, this being an exceptional feature among Ungulates. The great trochanter is very large, the second merely indicated by a roughened ridge. There is no trace of a third trochanter. The condyles are very large.

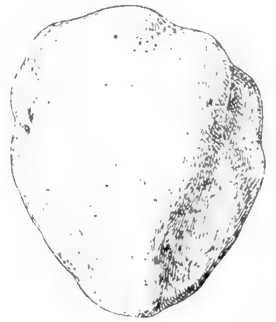

FIG. 14.—Left patella from Barrington, preserved in Sedgwick Museum, Cambridge. ⅓ natural size.

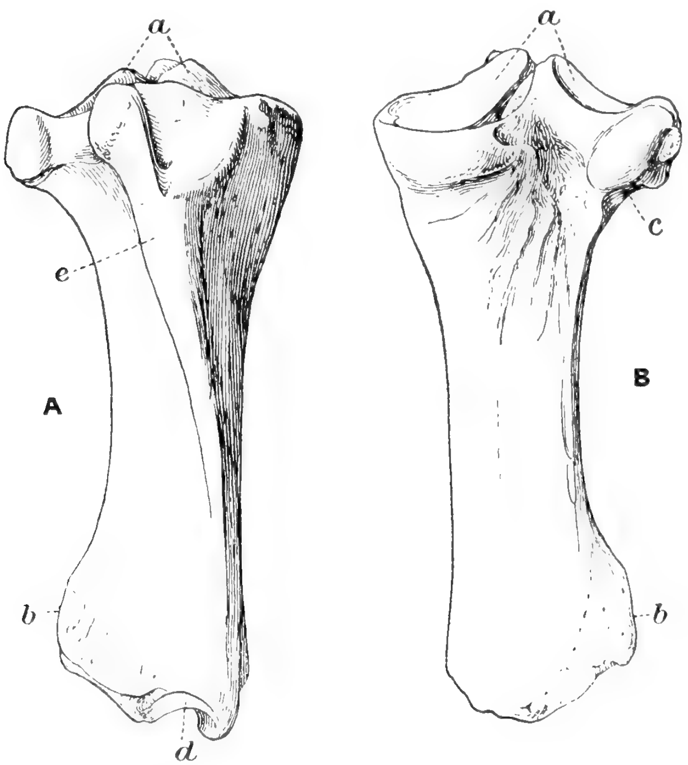

FIG. 15.—Right tibia. A front view; B seen from behind. ¼ natural size. From Barrington, preserved in the Sedgwick Museum, Cambridge. *a*, surfaces for articulation with condyles of femur; *b*, surface for articulation with distal end of fibula; *c*, surface for articulation with proximal end of fibula; *d*, surface for articulation with astragalus; *e*, cnemial crest.

The *tibia* is a very stout bone with the proximal end much expanded. The shaft is triangular in cross-section, and the cnemial crest very strong. The distal end is broad and somewhat compressed antero-posteriorly.

The *fibula* is a slender but distinct bone with a small proximal end and widely expanded distal end.

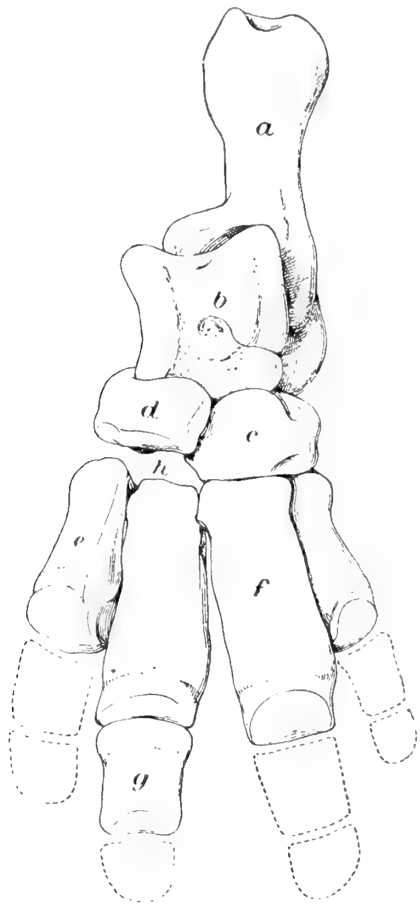

FIG. 16.—Front view of left pes of skeleton made up of bones from Barrington, mounted in Sedgwick Museum, Cambridge. ¼ natural size. *a*, calcaneum; *b*, astragalus; *c*, cuboid; *d*, navicular; *e*, 2nd metatarsal; *f*, 4th metatarsal; *g*, proximal phalanx of 3rd digit; *h*, space which should be occupied by the missing cuneiforms.

All the bones of the *tarsus* are separate. The large astragalus presents no special features, and the calcaneum is relatively shorter and stouter than in most artiodactyls. The cuboid and navicular are large bones. The internal cuneiform is missing and the middle is very small. A small pisiform is present

There is less uniformity in the length of the *metatarsals* than in that of the metacarpals, those of the 3rd and 4th digits being much longer than those of the 2nd and 5th. The ungual phalanges in each case are broad and flattened and a pair of sesamoid bones occur at each metatarso-phalangeal articulation.

TABLE OF MEASUREMENTS.

	Mounted skeleton 726n in Zool. Dept. of Brit. Mus.	Left femur from Whitstable, in Geol. Dept. of Brit. Mus.	Separate bones mounted in Zool. Mus., Cambridge.	Mounted skeleton from Barrington, in Sedgwick Mus., Cambridge (rt.).	Separate bones from Barrington, in Sedgwick Mus., Cambridge (rt.).
FEMUR.					
1. Length measured from head to internal condyle	47·6	57·75	46·2	50·35	54·0
2. Transverse diameter at condyle	13·5	18·5	15·05	17·15	16·05
3. Antero-posterior diameter of head	7·1	9·65	7·3	7·9	9·1
4. Antero-posterior diameter of middle of shaft	5·85	8·25	6·1	6·9	7·7
5. Transverse diameter at proximal end measured across head and great trochanter	15·75	20·2	16·6	16·8	19·65
TIBIA.					
1. Length	31·1	...	33·4	...	37·75
2. Right to left diameter at proximal end	14·05	...	15·35	...	17·0
3. Antero-posterior diameter at proximal end measured from notch between articular surfaces for femur to top of crest	9·3	...	10·0	..	11·7
4. Right to left diameter at distal end	9·3	...	9·6	...	10·75
FIBULA.					
1. Length	26·8	...	28·15		..
2. Antero-posterior diameter at proximal end	2·0	...	2·4	.	
3. Antero-posterior diameter at narrowest part of shaft	·9	...	1·25	..	...
4. Antero-posterior diameter at distal end	6·5	...	7·7	..	..
PES.					
1. Length of calcaneum	18·5	...	.	...	...
2. Maximum transverse diameter of calcaneum	7·8	..	.	..	...
3. Right to left diameter of astragalus measured at tibial articulating surface	7·1	..	...	...	...
4. Length of 2nd metatarsal	9·5	..	...	...	...
5. " 3rd "	12·8	...	.	...	...
6. " 4th "	13·5	...	...	...	...
7. " 5th "	9·8	...	...	...	..

IV. MUTUAL RELATIONSHIP OF THE HIPPOPOTAMIDÆ.[1]

Although so highly specialised in many respects, the hippopotami, as regards their limbs and grinding teeth, are the most primitive of living artiodactyls. The origin of the Hippopotamidæ is still obscure, and the earliest known species differ from the living *Hippopotamus amphibius* mainly in the slightly more generalised character of the incisors.

Stehlin,[2] basing his opinion chiefly on certain dental characters, has suggested

[1] For a synopsis of the Hippopotamidæ see Falconer, 'Palæontological Memoirs,' ii, p. 406.

[2] 'Abh. Schweiz. Pal. Gesell.,' xxvi, p. 433.

that *Acotherulum*, one of the Chœromoridæ, a group of primitive pigs, may indicate the source from which the hippopotami were derived. This form occurs in the Upper Eocene phosphorites of France. Osborn[1] has remarked on the affinity to the hippopotami of *Merycopotamus*, an animal originally described as a hippopotamus by Falconer and Cautley, but now placed near the Anthracotheres.

The situation of the region where the evolution of the hippopotami took place is unknown, but in view of the complete absence from the European Oligocene and Miocene deposits of ancestral forms, it must have occurred outside Europe. Stehlin and Forsyth Major[2] have suggested that the hippopotami, like the elephants, originated in Africa.

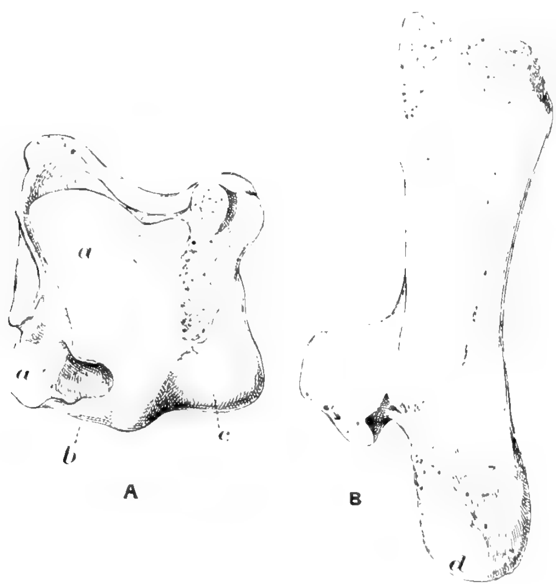

FIG. 17.—A left astragalus seen from behind. $\frac{1}{3}$ natural size. *a a*, surfaces for articulation with calcaneum; *b*, with cuboid; *c*, with navicular. B right calcaneum seen from behind. *d*, surface for articulation with cuboid.

The hippopotami suddenly appear in great variety in the Lower Pliocene beds of India, and by late Pliocene times had reached northern Africa and western Europe. A small hexaprotodont hippopotamus was described by Pantanelli[3] from strata probably of Lower Pliocene age from Casino near Siena.

The Indian species form a remarkable group and their affinities have been fully discussed by Lydekker.[4] He points out that specialisation has taken place along two main lines: (1) the shortening and widening of the mandibular symphysis frequently accompanied by a general shortening of the cranium and mandible; (2) the reduction in number of the incisors, this reduction probably occurring first

[1] 'Age of Mammals,' p. 313. [2] 'Geol. Mag.' [4], ix (1902), p. 197.

[3] 'Atti R. Accad. Lincei' [3], iii (1879), p. 318.

[4] 'Palæont. Ind.,' ser. 10, iii, p. 47.

in the lower jaw and being accompanied by a largely increased size in the case of one or more of the remaining pairs of incisors and of the canines.

The most primitive form of mandible is shown by *H. iravaticus*, in which the long narrow symphysis, three pairs of small incisors and small canines indicate an animal much closer to the pigs than any other species of which the mandible is preserved. The next step is seen in *H. sivalensis*, in which the symphysis is considerably shorter, though the incisors still preserve their small size. The third stage is found in *H. namadicus*, in which the symphysis has still more decreased in length, while $\overline{\text{i. 2}}$ has become slightly smaller and is thrown more or less above the level of the other two. Lastly, in *H. palæindicus* the symphysis is shorter than in any other form, while $\overline{\text{i. 1}}$ and $\overline{\text{i. 3}}$ have increased enormously in size at the expense of $\overline{\text{i. 2}}$. It is tempting to consider that *H. amphibius* was derived from *H. palæindicus* by the final disappearance of $\overline{\text{i. 2}}$, but, as has already been pointed out, the specimen No. 1873 in the Royal College of Surgeons Museum would seem to prove that the persisting teeth in *H. amphibius* are $\overline{\text{i. 1 and 2}}$, and further, Lydekker maintains that the long mandibular symphysis of *H. amphibius* shows that it could not have been derived from any of the Indian species. Its origin may perhaps be sought in the hexaprotodont *H. hipponensis* described by Gaudry[1] from Bone, Algeria. In *H.* (*Chœropsis*) *liberiensis* another incisor, probably the small one of *H. amphibius*, has disappeared.

Although Cuvier in the first instance believed the fossil hippopotamine bones to belong to *H. amphibius*, he quickly altered his opinion, considering that the fossil bones belonged to a larger extinct species which he named *H. major*. He was followed in this opinion by Nesti, Owen, Falconer, Forsyth Major, and originally by Boyd Dawkins.

The features in the fossil form on which these authors relied in separating it from the living species are—the larger size; wider interval between the second and third premolars; posterior position of the orbit; shortness of the cranium; greater elevation of the sagittal and occipital crests; excessive elevation of the upper margin of the orbit above the plane of the brow. Cuvier also states that the neck is shorter than in the living species, and that the width of the combined radius and ulna is only one-and-a-half times the length of the radius, instead of twice, as in the living species. By 1885 Boyd Dawkins was convinced as to the specific identity of *H. major* and *H. amphibius*, and many later writers, including Lydekker, have adopted the same view. De Blainville had arrived at the same conclusion as early as 1844. Osborn, however, in 'The Age of Mammals' (1910), retains the distinctive name *H. major* for the large fossil form, as does Forsyth Major (1896).

[1] 'Bull. Soc. Géol. France' [3], iv (1876), p. 501.

V. CONCLUSION.

In the present memoir no new material relating to the origin of the Hippopotamidæ is brought forward, and such new records as the memoir contains do not materially extend the known area of the distribution of the hippopotamus in Britain. The author agrees with Boyd Dawkins, Lydekker and others in regarding the *Hippopotamus major* of the Pleistocene as inseparable from *H. amphibius*. Evidence that the missing incisor tooth of *H. amphibius* is the third is brought forward.

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PLATE I.

PLEISTOCENE HIPPOPOTAMUS.

Hippopotamus amphibius.

Cranium.

(One-fourth natural size.)

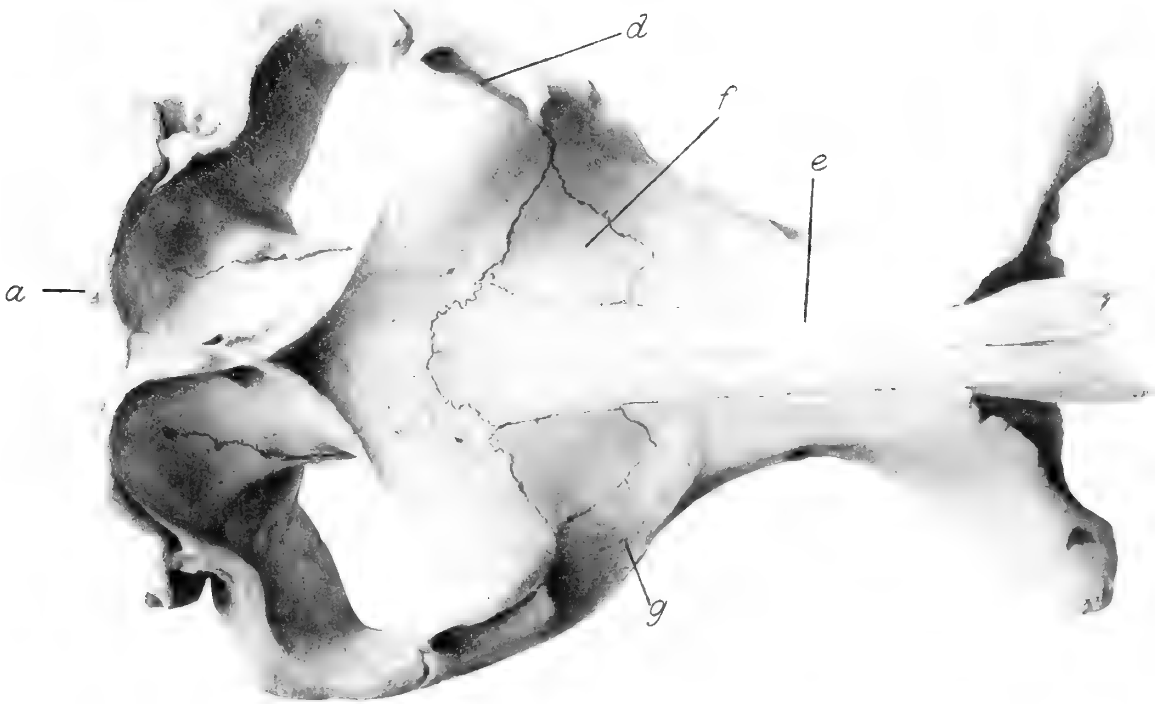
FIG.

1. Dorsal } view of a cranium from the river gravel of Barrington, near Cam-
2. Ventral } bridge.

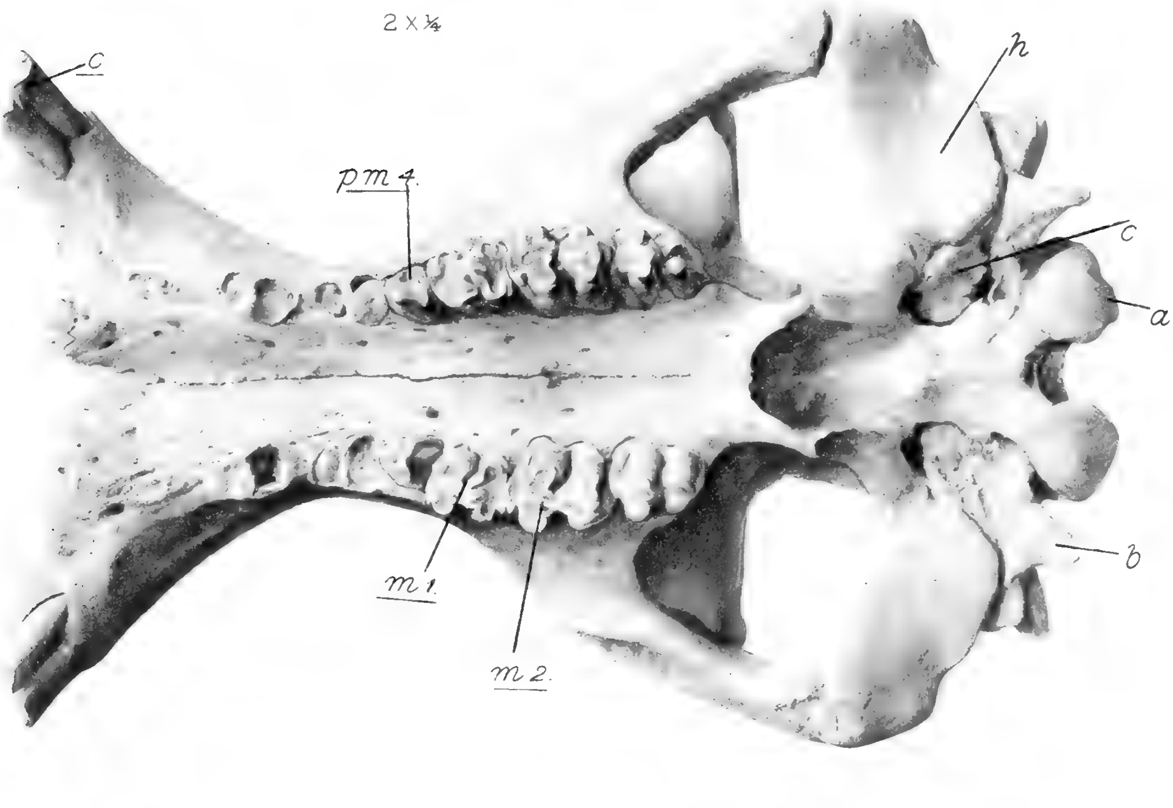
This is the cranium of the composite skeleton set up in the Sedgwick Museum, Cambridge. The premaxillæ are missing.

a. Occipital condyle.
b. Par-occipital process of exoccipital.
c. Tympanic.
d. Orbit.
e. Nasal.
f. Lachrymal.
g. Jugal.
h. Glenoid fossa.

1 X ¼



2 X ¼



HIPPOPOTAMUS AMPHIBIUS

Cranium.

J. Green del. London Stereoscopic Co. imp.

PLATE II.

PLEISTOCENE HIPPOPOTAMUS.

Hippopotamus amphibius.

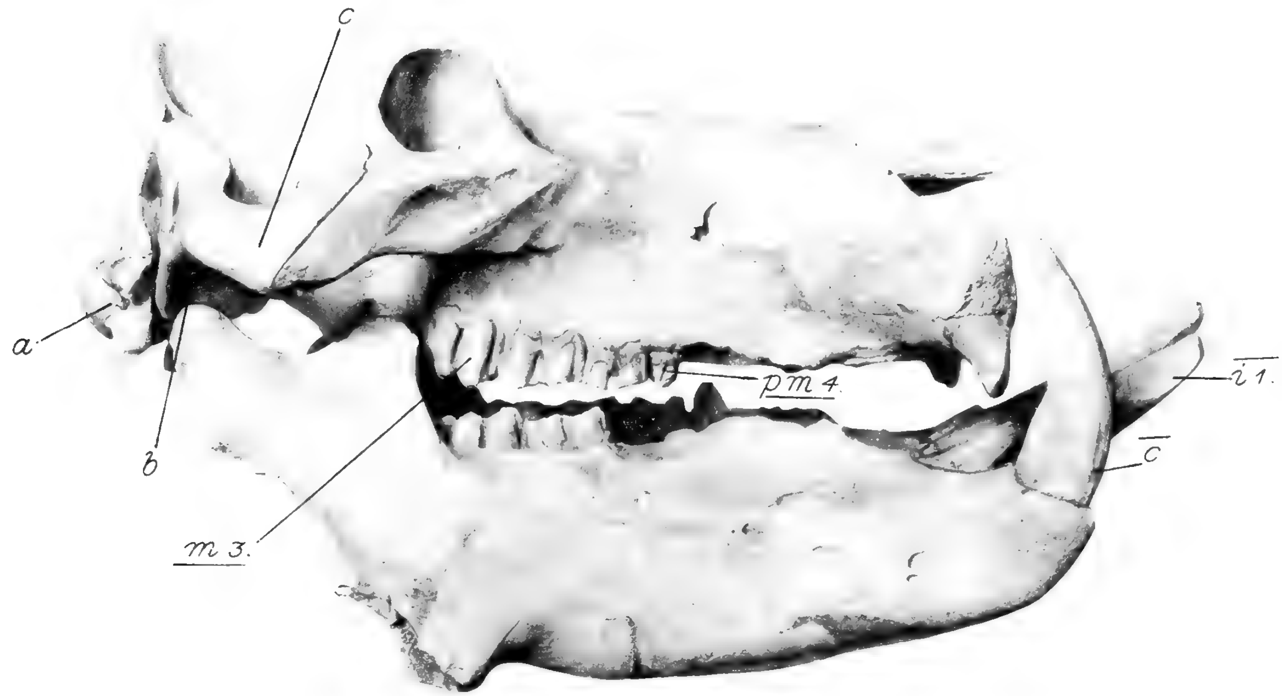
Skull.

FIG.		
1.	Skull seen from the right side (one-fifth natural size)	both from the river gravel of Barrington, near Cambridge.
2.	Mandible seen from the left side (one-fourth natural size)	

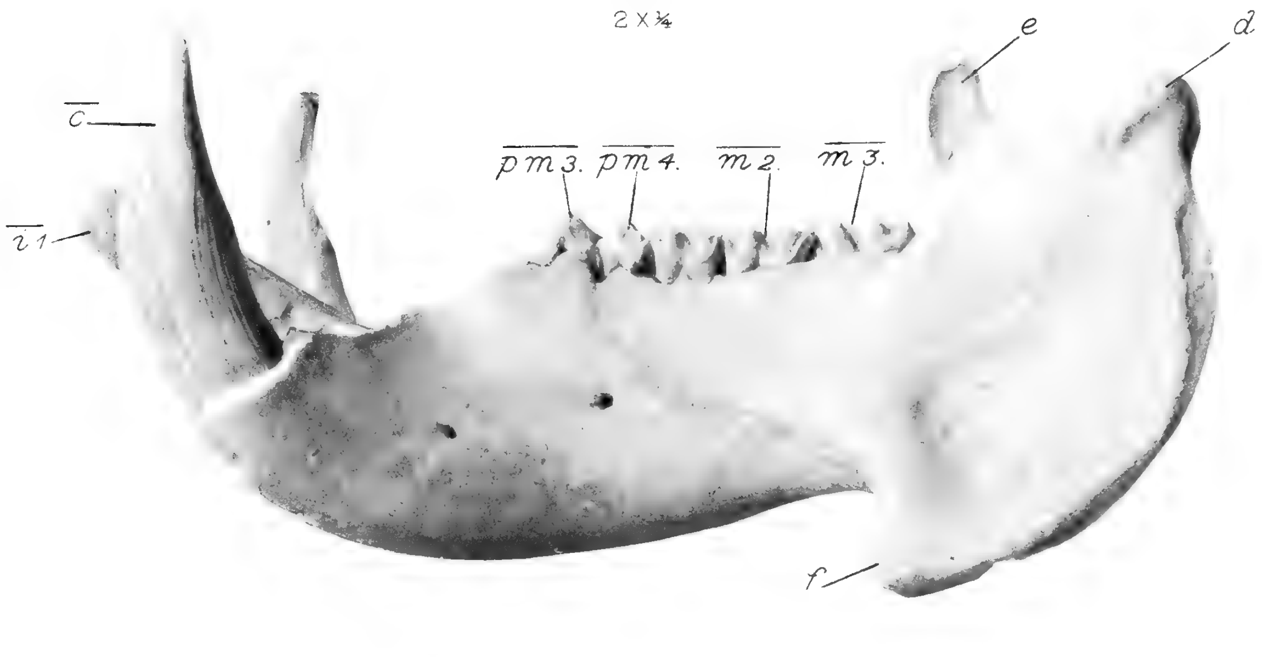
The skull, which lacks the premaxillæ, is that of the composite skeleton set up in the Sedgwick Museum, Cambridge. The separate mandible, which is also in the Sedgwick Museum, is labelled "Barrington 1884."

a. Occipital condyle.
b. Glenoid fossa.
c. Zygomatic process of squamosal.
d. Mandibular condyle.
e. Coronoid process.
f. Process from angle of mandible.

1 X 1/5



2 X 1/4



HIPPOPOTAMUS AMPHIBIUS

Skull.

J. Green del. London Stereoscopic Co. imp.

PLATE III.

PLEISTOCENE HIPPOPOTAMUS.

Hippopotamus amphibius.

Mandible.

(One-fourth natural size.)

FIG.

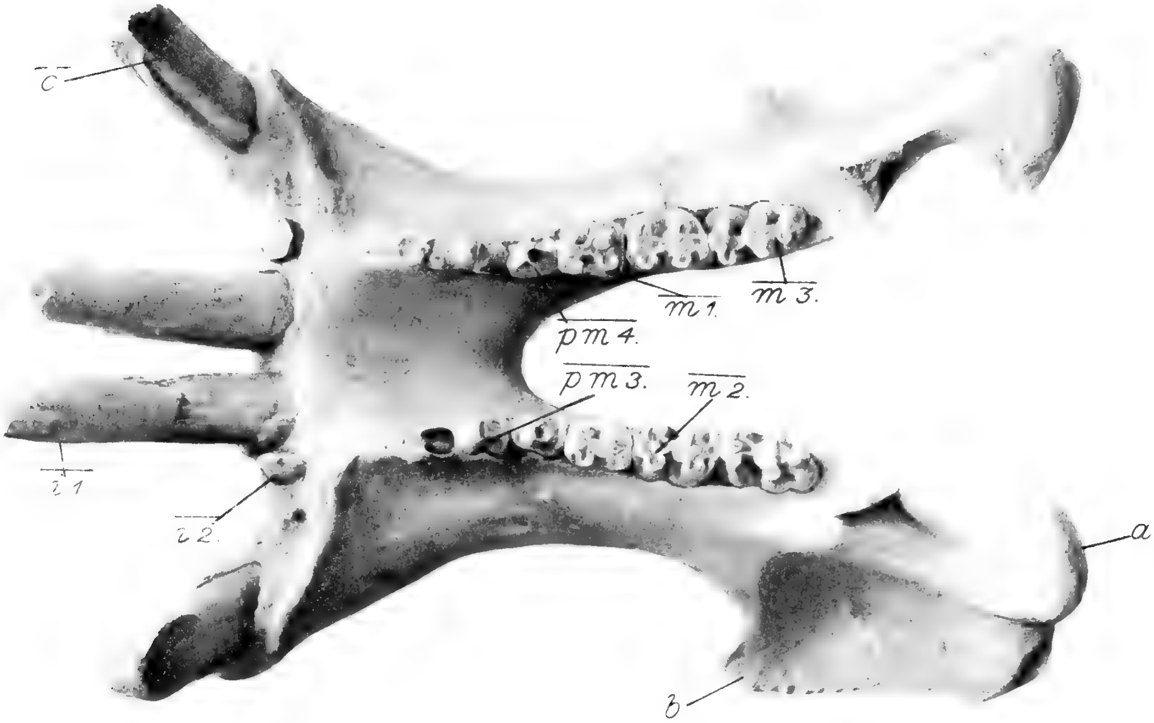
1. Palatal view of mandible (Barrington, 1884).
2. Right side view of mandible (Barrington, 1888).

Both from the river gravel of Barrington, near Cambridge, and preserved in the Sedgwick Museum.

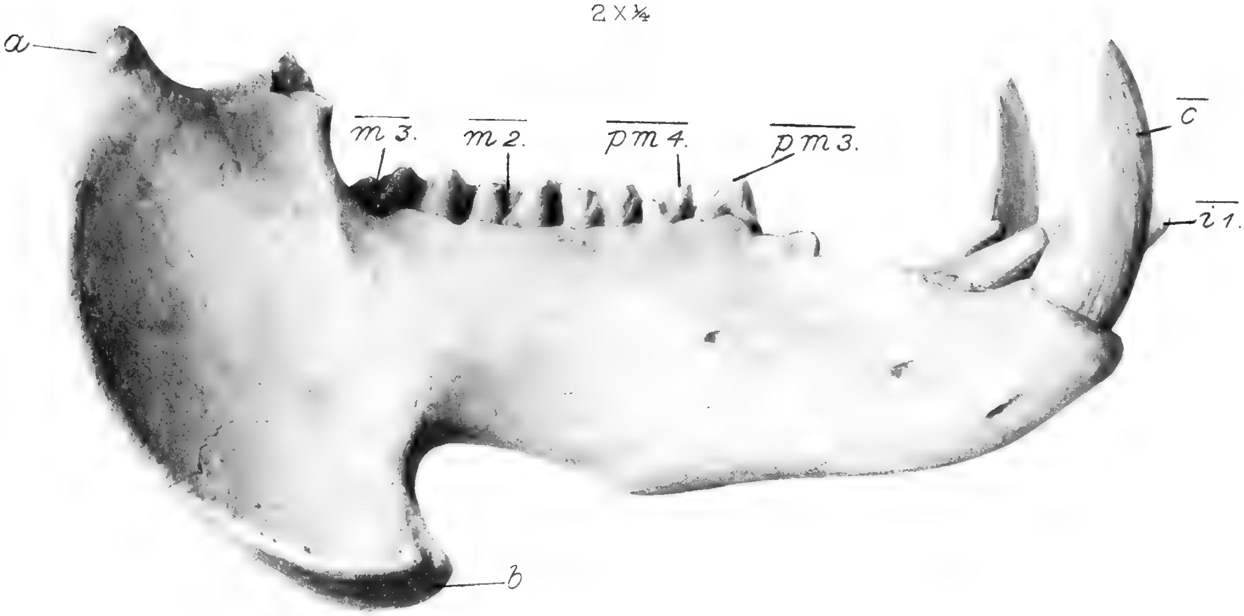
a. Mandibular condyle.

b. Process from angle of mandible.

1 X ¼



2 X ¼



HIPPOPOTAMUS AMPHIBIUS.

Mandible

J. Green. del. London Stereoscopic Co. imp.

PLATE IV.

PLEISTOCENE HIPPOPOTAMUS.

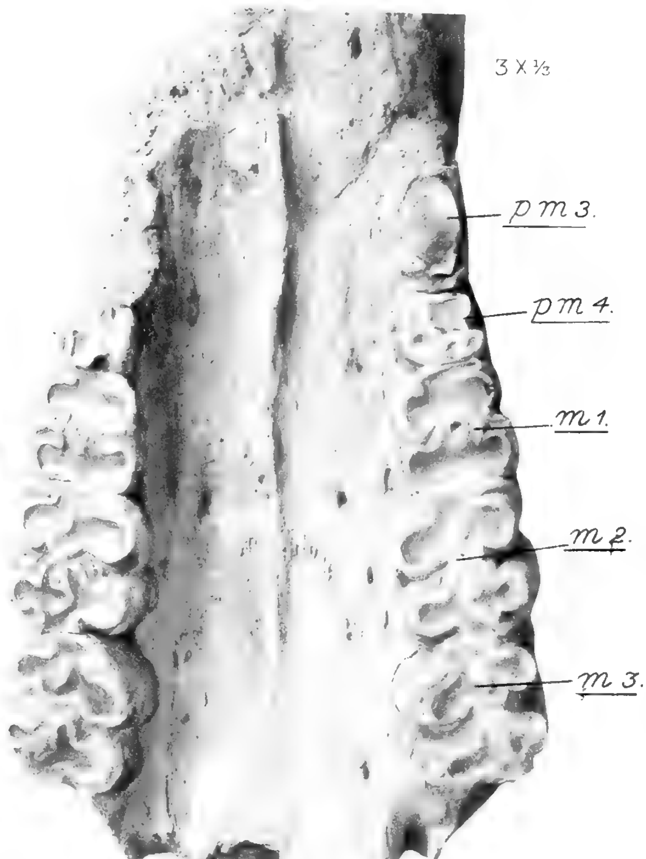
Hippopotamus amphibius.

Mandible and Upper Premolars and Molars.

FIG.

1. Palatal view of mandible (Barrington, 1888). (One-quarter natural size.)
2. Oblique view of end of mandible. (One-fifth natural size.)
3. Palatal view of fragment of upper jaw. (One-third natural size.)

All are from the river gravel of Barrington, near Cambridge, and are preserved in the Sedgwick Museum. From the relatively slight development of the canines and first incisors, it may probably be concluded that the mandible (fig. 1) is that of a female.



HIPPOPOTAMUS AMPHIBIUS

J. Green del. Mandible & Upper Premolars & Molars London Stereoscopic Co. imp.

PLATE V.

Pleistocene Hippopotamus.

Hippopotamus amphibius.

Chiefly Permanent Dentition.

(All two-thirds natural size.)

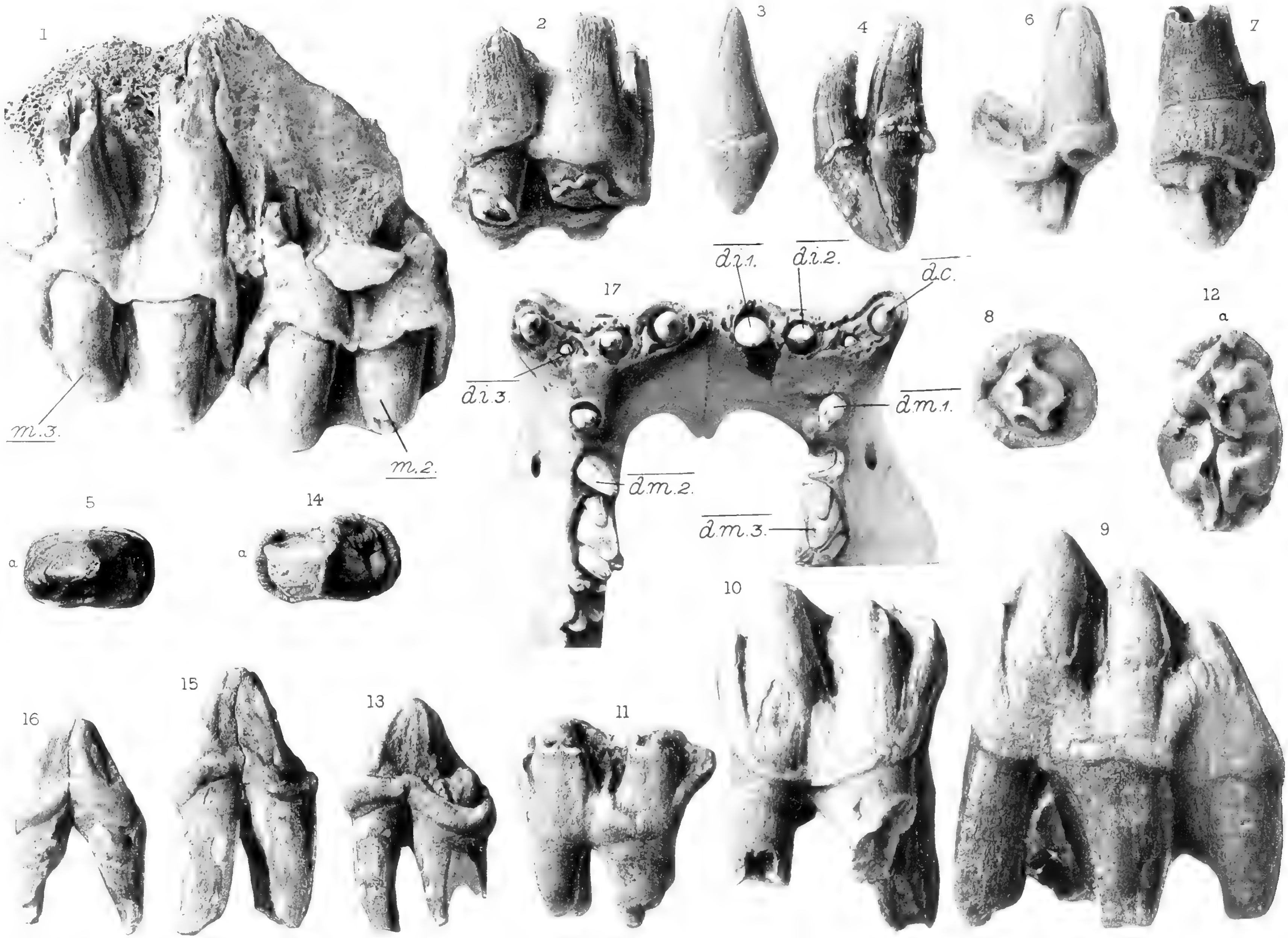
a = Anterior end of tooth.

Fig.

1. Fragment of right maxilla with m. 2 and 3 little worn, outer side. (S.)
2. Left m. 1, worn, inner side. (B.M.)
3. Right pm. 1, unworn, inner side. (S.)
4. Left pm. 2, unworn, outer side. (S.)
5. The same tooth, oral aspect.
6. Right pm. 3, inner side. (B.M.)
7. Right pm. 4, unworn, inner side. (S.)
8. Right pm. 4, somewhat worn, oral aspect. (S.)
9. Right m. 3, unworn, inner side. (S.)
10. Right m. 2, rather worn, inner side. (S.)
11. Right m. 1, a good deal worn, inner side. (B.M.)
12. Right m. 1, unworn, oral aspect. (B.M.)
13. Right pm. 4, unworn, inner side. (S.)
14. Left pm. 3, oral aspect. (S.)
15. Right pm. 3, unworn, inner side. (S.)
16. Right p.m. 2, slightly worn, inner side. (S.)
17. Palatal view (natural size) of anterior end of mandible of a newborn hippopotamus showing the milk-dentition in position. The germ of d.i. 3 is visible. This specimen is no. 1873 in the catalogue of the Museum of the Royal College of Surgeons.

With the exception of no. 17, which is a recent specimen, all the above are from the river gravel of Barrington, near Cambridge. Those marked "S." are preserved in the Sedgwick Museum, Cambridge; those marked "B.M." in the British Museum.

Reynolds, Pleistocene Hippopotamus. PL. V.



J. Green del. London Stereoscopic Co. imp.

HIPPOPOTAMUS AMPHIBIUS.

Chiefly Permanent Dentition × 2/3

PLATE VI.

PLEISTOCENE HIPPOPOTAMUS.

Hippopotamus amphibius.

Chiefly Milk-Dentition.

(All natural size, except figs. 1—3.)

a = Anterior end of tooth.

FIG.

1. Fragment of right maxilla with 4 teeth, outer view. } (S.) (two-thirds natural size.)
2. The same, oral aspect.
3. Small fragment of right maxilla with m. 1 and 2 (much worn), oral aspect. (S.) (Two-thirds natural size.)

Upper Milk-Teeth.

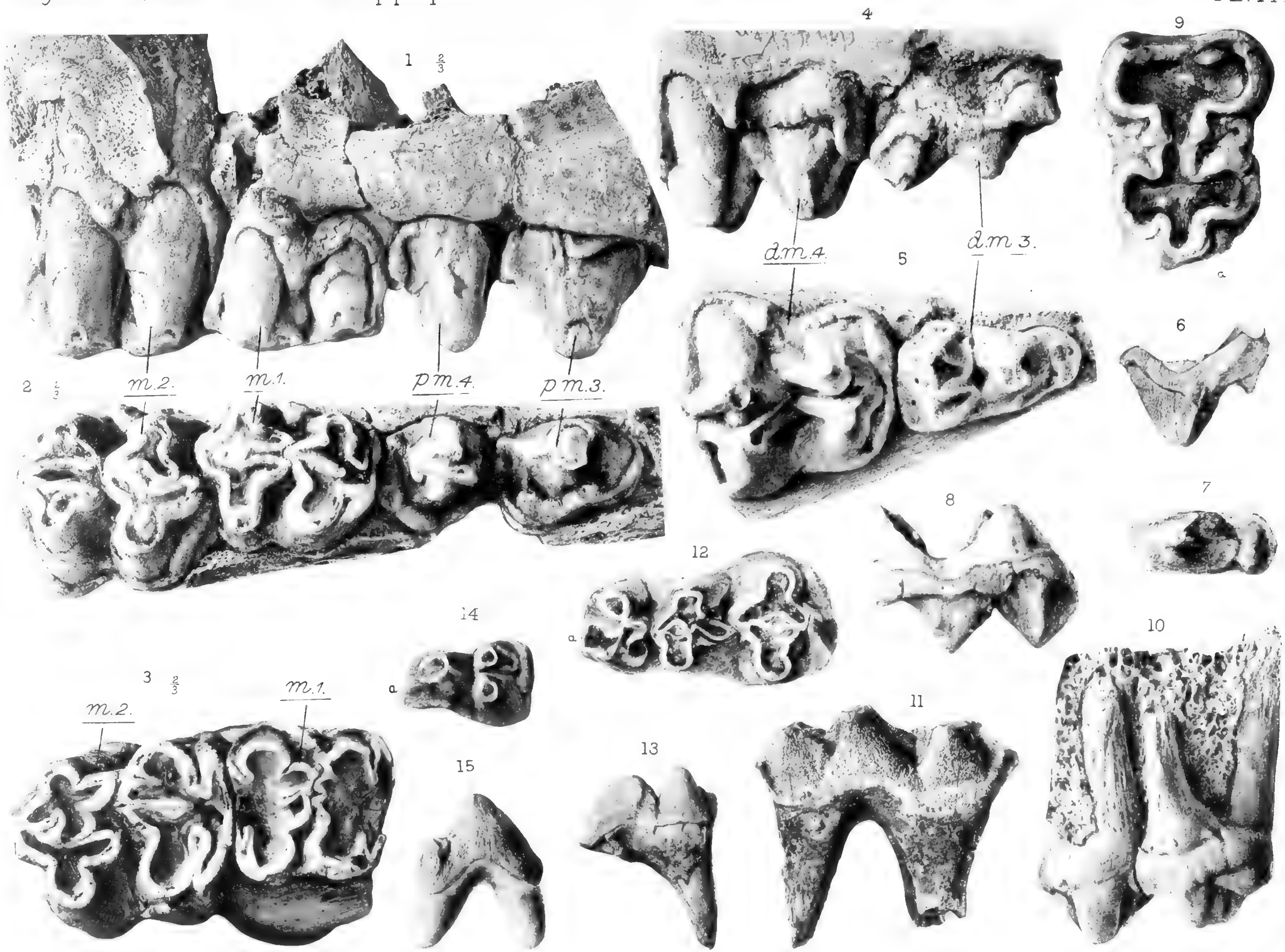
4. Fragment of right maxilla with dm. 3 and 4, outer view. (S.)
5. The same, oral aspect.
6. Dm. 2, right, unworn, inner side. (B.M. $\frac{M.}{4009}$.)
7. The same, oral aspect.
8. Dm. 3 (right), unworn, inner side. (B.M. $\frac{M.}{4646}$.) Widger Coll., Torbryan, Torquay.
9. Dm. 4, right, worn, oral aspect. (S.)
10. Fragment of bone with dm. 4 (left), inner side showing roots of teeth. (S.)

Lower Milk-Teeth.

11. Dm 4, right, worn, inner side. (S.)
12. The same, oral aspect.
13. Dm. 3, right, somewhat worn, inner side. (S.)
14. The same, oral aspect.
15. Dm. 2, right, unworn, inner side. (B.M. $\frac{M.}{4009}$.)

All the above specimens, with the exception of no. 8, are from the river gravel of Barrington, near Cambridge. Those marked "S." are preserved in the Sedgwick Museum, Cambridge; those marked "B.M." in the British Museum.

Reynolds, Pleistocene Hippopotamus. PL. VI.



J. Green. del. London Stereoscopic Co. imp.

HIPPOPOTAMUS AMPHIBIUS.

Chiefly Milk Dentition